THE INFLUENCE OF SOIL FERTILITY AND LIGHT INTENSITY ON FIELD LAYER DEVELOPMENT IN URBAN SECONDARY WOODLANDS

Marion Jane Bryant B.Sc., M.Res.

2003

A thesis submitted in partial fulfilment of the requirements of the University of Wolverhampton for the degree of Doctor of Philosophy

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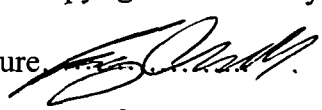
Signature 

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Undergrowth. Vincent van Gogh. 1887.

Abstract

The study investigated the influence of soil fertility and light climate on field layer development in urban secondary woodlands with an introduced ground flora, with the aim of contributing towards ground flora enhancement methodology and sympathetic secondary woodland management.

The investigation was based on a series of complementary field and greenhouse replicated plot, single and multiple factor experiments. Multivariate analyses of vegetation response and measurements of soil fertility, light climate and other environmental variables were used to examine the influence of soil fertility and light climate in combination and in interaction on field layer community establishment from seed.

Light intensity (PAR) was a major determinant of ground flora development and was readily manipulated by canopy thinning. Optimum dark phase irradiance, for the successful establishment of introduced species, was 5-20% of ambient PAR (photosynthetically active radiation). This was achieved in both field experiments by removing 50% canopy cover from varied canopy starting points (i.e. simple monospecific *vs*. multi-layered mixed).

All introduced species grew well across the full range of soil conditions in the experimental programme. Soil fertility was a major determinant of field layer development, although its influence was usually secondary to that of light intensity. The relative importance of different aspects of soil fertility were less predictable than those of the light climate. Fertilisation enhanced nutrient uptake and ground flora establishment in woodland plots, which were buffered from edge effects, although fertilisation is unlikely to prove viable or ethical in most woodland restoration schemes.

The interaction between soil fertility and light intensity enhanced introductions in the field, but reduced their success in the artificial ground flora communities of the polytunnel, encouraging negative competition from arable weeds. High soil fertility appears not to be such an obstacle to diversity in woodland as it is in grassland restoration schemes, provided that the stand is protected from edge effects by a large buffer zone, ensuring adequate distance from weed seed sources. Sites where high soil fertility and irradiance combine are liable to domination by the non-woodland grasses, necessitating herbicide pre-treatment, which will reduce rather than enhance, existing niche heterogeneity.

Thinning, and the associated disturbance, influenced light intensity, soil fertility (e.g. by increasing mineralisable nitrogen) and other environmental variables which combined to determine niche space. Thinning can be used to augment the existing niche heterogeneity provided by the canopy, litter layer, spontaneous vegetation and background soil environment. Optimal litter cover was 15-40% and optimal cover of bare ground and bryophytes were within the range 10-40%. It is recommended that no sub optimal environmental variable cover be over 25% of site area and that a mosaic effect is sought.

Acknowledgements

This work is dedicated to Robbie Gray (1945-2001), Professor of Social History at the University of Portsmouth and loving husband to my mother. Thank you for your encouragement and words of wisdom. Perhaps one day I will be able to enhance the ground flora in your woodland. Rest in Peace.

I would like to thank my Director of Studies Dr Eleanor Cohn, who inspired me to 'take a leap into the shade', i.e. from grassland to woodland research, and I am very grateful for, and humbled by the experience. Thank you for your guidance, support and faith in me. I would also like to thank the rest of my supervisory team, Professor Ian Trueman and Dr Mike Fullen for their ideas, advice and encouragement. It has truly been a privilege working with you all.

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Chapter 1: Introduction and Literature Review

1.1 Introduction and background to the current research

The current research investigates the influence of the interaction between soil fertility and light intensity on ground flora development following species introductions in urban secondary woodlands. The information gained contributes towards woodland habitat creation practice by defining environmental boundaries within which success is probable. This knowledge will also be useful in providing informed management plans for existing secondary woodlands. Buckley (1989) defined habitat reconstruction as aiming to establish plant communities which in some way resemble the semi-natural original. The aim of habitat reconstruction is central to the current study and previous work in the field of woodland habitat creation and restoration.

1.2 Woodlands in the UK

1.2.1 Types of woodland

1.2.1.1 Ancient semi-natural woodland

Woodland is the climax vegetation of post-glacial Britain and has come about through the interactive processes of succession and competition since the last Ice Age. The term 'wildwood' is given to the primary forest which colonised much of post-glacial Britain, before the impacts of human occupation were felt (Rackham, 1990). This colonisation occurred in waves, as the climate warmed and sea levels rose creating the barrier of the English Channel, with different suites of species colonising and later becoming out-competed by species more suited to the prevailing environmental conditions. These processes of succession eventually stabilised and pollen analysis dates the climax wildwood to *c.* 4500 BC (Rackham, 1990). This wildwood varied regionally and locally in species composition, as woodlands do today, according predominantly to climate and soil type (Kirby, 1992). The structure of this wildwood depended largely on the type of regeneration gaps left by the demise of dominant canopy species (Rackham, 1990). The pollen record of field layer species indicates that many contemporary species existed in the wildwood, e.g. *Hyacinthoides non-scripta* and *Rubus fruticosus* agg. This record also shows that the wildwood was not continuous, but forest interspersed with glades where a non-shade-tolerant ground flora dominated. The term 'ancient woodland' implies habitat continuity with the wildwood, which has largely been destroyed by human activity (Section 1.2.2). Kirby (1992) defined ancient woodlands as those which do not appear to have been cleared in the last 400 years. Some of these ancient woods are continuous with

the wildwood, whereas others represent secondary succession following field abandonment in Roman or Medieval times. The adjective 'semi-natural' refers to the influence which human management has had on these fragments of ancient woodland (Section 1.2.2).

1.2.1.2 Secondary woodland

Secondary woodland can be defined as land which has experienced a break in woodland cover in its history (Kirby, 1992). This could be, for example, due to grubbing out trees for agriculture followed by secondary succession or planting. Many secondary woods are in fact plantations. Mature secondary woodland differs from ancient semi-natural woodland by having less structural and floristic diversity (Section 1.3). The canopy tends to be fairly unstructured and even-aged often casting dense shade. This shading coupled with low colonisation of woodland herbs (Section 1.3) leads to impoverished ground floras, which will probably lack ancient woodland indicator species (Peterken, 1993). Hodge and Harmer (1996) reported that secondary succession on urban sites in the West Midlands led to species-poor canopies, which could have implications for ground flora diversity.

1.2.2 Losses of ancient semi-natural woodland

Today only fragments of the ancient 'wildwood' remain (Kirby, 1992) and its decline has been well documented by workers like Rackham (1980, 1990) and Peterken (1993). Destruction of the wildwood for agricultural clearance began in the Neolithic period, just prior to the elm decline, and accelerated with population increase until the early Iron Age. Although the fertile valley soils would have been favoured for agricultural production, clearance was extended to the uplands during the Bronze Age, where later abandonment and climate change led to the development of moorland. Records from the Domesday Book indicate a medieval landscape of isolated and fragmented woodlands within a farmland matrix (Kirby, 1992). From Neolithic times onwards parts of the wildwood were managed for timber and underwood production rather than being grubbed out. Extant ancient woodland fragments have been much influenced by human intervention in the form of management, such as coppicing and other forms of timber production plus grazing of stock and are therefore referred to as ancient semi-natural woodland (Kirby, 1992). Decline of British semi-natural vegetation has been particularly rapid in recent times, and is especially due to agricultural change since the last war. For example, since 1930 46% of ancient semi-natural broad-leaved woodland has been lost, mainly due to

coniferisation. Today less than 14% of existing woodland can be described as ancient semi-natural (Ratcliffe, 1984).

Coppice management prevents long term canopy closure as in 'high forest' management (e.g. Kirby, 1992) and it promotes proliferation of the less shade tolerant ground flora species, such as *Hyacinthoides non-scripta* (Blackman and Rutter, 1954) early in the rotation. It is likely that the mosaic of light and shade produced by coppicing existed within the wildwood on a smaller scale. Many herbs found in today's ancient semi-natural woodland are relicts from the wildwood. Evidence from pollen cores and plant remains substantiate this for species such as *Circaea lutetiana* and *Oxalis acetosella* (Peterken, 1993). It seems reasonable to conclude that past management (especially coppicing) has ensured survival of such species in woodland fragments often too small to sustain the range of environments needed under high forest (e.g. Barkham, 1992). Peterken and Francis (1999) noted that woodland scale is important in the distribution of open space and in the conservation of non-woodland species, which have become extinct from the surrounding countryside. Reader and Bricker (1991) found that the effects of the scale of thinning operations on ground flora species distributions were inconclusive. Peterken (1993) referred to the decline of coppicing in the nineteenth century, which has led to impoverishment of ground flora communities. Therefore, the problem is not only one of habitat loss, but also of fragmentation, scale and loss of quality of habitats which persist.

1.2.3 Woodland classification

Ancient semi-natural woodland takes many forms in Britain. Classification of this diversity has been attempted by Peterken (1993), Tansley (1939) and most recently Rodwell (1991) in the form of the National Vegetation Classification (N.V.C.). Climate and soils are universally found to be the most important determinants of woodland type. All of the above workers acknowledge the relative influence of historic silvicultural practices in terms of impacts on species composition and structure.

1.3 Differences between ancient and secondary woodlands

Species which colonise secondary woodlands differ from those characteristic of ancient semi-natural woodland, both in appearance and in their biological and ecological attributes. Most ancient woodland herbs are very poor colonisers for several reasons: they tend not to be competitive and are usually stress tolerators in the Competitor – Stress

tolerator – Ruderal (C-S-R) model of ecological plant strategies (Grime, 1979). These species have developed adaptations to tolerate the woodland stresses of shade (Packham and Willis, 1976, 1982) and leaf litter (Salisbury, 1916; Sydes and Grime, 1981a,b). Although shade and litter levels both depend on canopy type, shade is probably the single most important constraint on plant growth within the woodland environment (Packham *et al.*, 1992). Ancient woodland herbs tend to grow slowly and often depend more on vegetative expansion than seed production (Salisbury, 1976). When seeds are produced they tend to be relatively few in number, large, heavy and poorly dispersed (e.g. Salisbury, 1942; Packham and Cohn, 1990). Poor dispersal mechanisms interact with the spatio-isolation of parent plants and the availability of suitable germination niches (Dzwonko, 2001; Verheyen and Hermy, 2001), greatly reducing the possibilities for colonising new woodlands (Buckley and Knight, 1989). Petersen (1994) splits ancient semi-natural woodland herbs into four functional groups: 1. Species favoured by traditional woodland management. 2. Species restricted to woodlands where specific environmental (e.g. soil) conditions have had sufficient time to develop. 3. Species with limited ability to spread or establish. 4. Species which in ancient woodland are represented by small and scattered populations.

Harmer *et al.* (2001) characterised the development of woodland ground flora, during 100 years of uninterrupted secondary succession on arable land, by: 1. A high species turnover. 2. A failure of local shade-bearing species to colonise. 3. The inability of some colonists to spread beyond the woodland margins. This appeared to be associated with: 1. Dense shade from the closed canopy. 2. Competition from established ground flora dominants, particularly *Hedera helix*. 3. Lack of suitable moist soils and open space habitats within the woods. 4. Acidification of soils. Verheyen and Hermy (2001) found that the presence of *Urtica dioica* restricted colonisation by ancient woodland herbs.

Plant colonisers of secondary woodland tend to be competitive ruderals (Grime *et al.*, 1988) which are fast growing and nutrient demanding. They commonly reproduce by seeds which are usually small, numerous and widely dispersed. They are therefore capable of colonising distant habitats and are also tolerant of the disturbance which is a feature in the history of many secondary woodlands. Competitive ruderals such as *Urtica dioica, Anthriscus sylvestris* and *Epilobium* species (willowherbs) which are moderately shade-tolerant can persist at high nutrient levels under relatively dense shade. (Although Grime *et al.* (1988) class *Urtica dioica* as a competitor they acknowledge its colonising

abilities in productive, heavily-disturbed vegetation). Urban substrates are often nutrient rich (Gilbert, 1989). This would indicate that the balance between soil fertility and light intensity is critical in determining the type of vegetation which develops.

Time is the major factor in woodland development that cannot be reconstructed. The woodland assemblage characterised as *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland community (W8) formed over millennia (Rodwell, 1991) and it is likely that a minimum of centuries would be required for spontaneous development of ground flora communities representative of ancient semi-natural woodland. Francis (1995) believed that even after centuries of secondary succession, target ground flora communities (Section 1.4.1) cannot necessarily be expected. However, Harmer *et al.* (2001) reported the development of W8 type communities on abandoned arable land, in Hertfordshire, after 100 years of secondary succession. The field layer transition from a mainly light-demanding flora to a shade-tolerant woodland flora occurred within 20-40 years of abandonment. Petersen (1994) found that the woodland summer light climate was darker, soil pH was lower and soil organic content matter high, in ancient semi-natural woodlands (>200 years old) compared to secondary woodlands (25 - ~100 years old) in Denmark. The field layers in the ancient woodlands were dominated by spring flowering geophytes (vernal species), whereas short-lived species, and few vernal species, characterised the secondary woodland field layers.

The propagule source of plants characteristic of ancient semi-natural woodland must be considered in woodland restoration schemes. Even after 70 years of secondary woodland development adjacent to ancient semi-natural woodland, ground floras in the Western Carpathian foothills were still divergent (Dzwonko, 1993; Dzwonko and Gawronski, 1994). Restoration of recently wooded sites should consider the soil seedbank as a potentially viable source of propagules. Pigott (1990) showed that dormant seed of vernal species persisted for at least 25-30 years when a conifer nurse crop (used to establish oak and beech in old woodland) had severely impoverished the former field layer. McLachlan and Bazely (2001) concluded that 'highly vulnerable species' (including vernal species with gravity-dispersed seeds) are likely to have to be 'actively reintroduced' in woodland restoration schemes. In woodland habitat creation the aim is to speed up succession (Packham *et al.*, 1992) via introductions of target ground flora species (Section 1.4.1).

1.4 The rationale for woodland habitat creation

Woodland habitat creation is justified by its contribution towards achieving the two main aims of habitat reconstruction, i.e. to counter semi-natural habitat loss and to improve amenity. The ground flora is an integral part of the target ecosystem (Section 1.4.1) and its selective introduction will speed up succession towards the target community. In the absence of species introductions into secondary woodlands, the poor-colonising characteristics of the woodland herbs (Section 1.3) will lead to long-standing biologically impoverished field layers (Cohn *et al.*, 2000). Woodland field layer translocation has been attempted by Helliwell *et al.* (1996), using topsoil, but this was only partly successful at transferring target species and involved the destruction of the ancient semi-natural woodland source site. This may be acceptable in isolated cases where a valuable site is to be lost to development, however, only a cost effective and sustainable method of sourcing and introducing woodland ground flora species into secondary woodlands will be applicable on a wider scale. Woodland ground flora enhancement allows utilisation of suitable existing ground flora and hence creation of more naturalistic and representative target communities (Section 1.4.1).

The creation of aesthetically pleasing plant communities in urban areas, where wildlife is often impoverished, is important as it promotes enjoyment of public open spaces and improves the standard of living for those in the neighbourhood. Woodland habitat creation, especially in population centres such as the West Midlands, offers some level of protection to ancient semi-natural woodlands as it partly relieves visitor pressure on such sites. Created woodlands provide a public educational resource and an invaluable research tool which informs the objective of habitat reconstruction. Manipulation of field layer communities facilitates investigation of their dynamics, a better understanding of which will inform the management of ancient semi-natural woodland sites. These created woodlands also provide potential low maintenance landscapes that are favourable to local authorities on tight budgets who cannot always deliver complex management plans (Cohn, 1998).

There are, of course, arguments against habitat reconstruction. For example, poorly planned species introductions could cause genetic contamination of local plant populations, disrupting natural geographic distributions and therefore leading to a loss of ecological information. In order to combat these potential problems, only native species of local provenance should be used. Urban habitats often have intrinsic ecological value

or the potential to develop it (Gemmell, 1982). There is a philosophical argument that successful habitat creation schemes will lead to destruction of semi-natural habitats, as developers promote the idea that semi-natural habitats are replaceable. This belief can be countered by targeted research and wider dissemination of findings.

1.4.1 Target communities

The definition of Buckley (1989) of habitat reconstruction implies definition of a semi-natural target community. The target community for the purposes of this research is the *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland community (W8), described by Rodwell (1991). W8 is the commonest woodland type on lowland base rich soils (Rodwell, 1991) and the urban substrates, which are likely to be the target of habitat reconstruction, such as concrete or brick rubble, are often extremely base-rich (Gilbert, 1989). Rodwell (1991) believed that, over much of its range, W8 probably represents the climax forest type of more base rich soils and has almost universally been affected by silvicultural treatment, often in the form of coppicing. It is this treatment which blurs the largely edaphic boundaries between sub-communities within W8 (Rodwell, 1991). Target communities are composed partly of target species, in this case the poor-colonising woodland herbs, and for the purposes of ground flora enhancement can be derived from the W8 floristic table (Rodwell, 1991). Species introduced in ground flora enhancement schemes need to be easy and cheap to establish over a wide range of environmental conditions (Section 1.5.2).

1.5 Habitat reconstruction in practice

1.5.1 Habitat reconstruction

Reconstruction of different habitats such as grassland (e.g. Wells *et al.*, 1986; Trueman *et al.*, 1994), heathland (Marrs, 1992), pasture woodland (Austad and Skogen, 1990) and woodland field layers (Boorman, 1990; Francis *et al.*, 1992; Cohn and Packham, 1993; Humphrey, 1996) have been attempted. High residual soil fertility is widely believed to be a major barrier to successful habitat reconstruction and various techniques have been employed to overcome this problem, such as topsoil stripping or inversion, via deep ploughing, cropping, including grazing and burning, and chemical treatment (e.g. Marrs, 1993; McCrea *et al.*, 2001a). However, habitat reconstruction has traditionally been little researched, being more a product of trial and error than the application of scientific knowledge (Buckley, 1989). A lack of monitoring of schemes (Gilbert and Anderson, 1998) has hindered formation of a sound research base for habitat reconstruction. There

has also been little attempt to prescribe long term management to maintain or enhance created diversity.

The present research was undertaken within the University of Wolverhampton Habitat Creation and Vegetation Ecology Research Group, working in collaboration with Wolverhampton City Council, Wrekin Council and Groundwork Black Country. The group's previous experience in the creation and management of semi-natural habitats (e.g. Jones *et al.*, 1990; Atkinson *et al.*, 1995; Cohn, 1994) has illustrated that distinctive plant communities can be created in new habitats, but that the maintenance of appropriate levels of species diversity depends on the management of stress and disturbance factors, such as mineral nutrient availability, shade and cropping to prevent dominance by competitive species, as predicted by the C-S-R model of Grime (1979).

In a review of terrestrial habitat creation, Jones (1990) found that only 11.8% of schemes were woodland creation and most involved tree planting only. New secondary woodland is a visually barren environment and weed control aimed at enhancing tree establishment often compounds this effect (Slater and Drake, 1988). However, this is usually rapidly superceded by development of a vigorous ruderal field layer, particularly on fertile urban or ex-arable sites (Cohn and Millet, 1995; Francis, 1995).

1.5.2 Woodland field layer enhancement

Kirby (1992) acknowledged the need for research into ground flora enhancement within new woodland plantings. Woodland field layer enhancement is a fairly new area of research and has been attempted by relatively few workers. Field layer enhancement will only 'counter semi-natural habitat loss' if the communities created are representative of target communities (Section 1.4.1) and serve some of the functions of semi-natural communities, such as enhanced wildlife and amenity (Cohn, 1998). Francis *et al.* (1992), Cohn and Packham (1993) and Cohn (1994) have illustrated that field layer herbs can be successfully introduced into urban woodlands and that in time they can produce distinctive plant communities which are diverse, resilient, attractive and natural-looking (Cohn *et al.*, 2000).

The work of Francis (1993) and Cohn (1994) refined the selection of target species by identifying woodland herbs which could be readily introduced into secondary woodlands with a variety of environmental conditions. Long-term observations showed that these

species were able to persist in competition with spontaneous vegetation and would go on to form self-perpetuating ground flora communities (Cohn *et al.*, 2000). These observations also identified species, like *Geum urbanum* and *Stachys sylvatica* which, although desirable components of the target community W8 (Rodwell, 1991) (Section 1.4.1) are very vigorous and not suitable for introduction. Species such as these may well colonise secondary woodlands without introduction.

In reviewing the regenerative strategies of the target species, conducting germination trials and establishment experiments, Cohn (1994) identified the most appropriate methodologies for introducing these species into secondary woodlands. Autumn sown seed was found to be the preferred method of introduction for species principally reproducing by seed. Of the species studied, only *Lamiastrum galeobdolon* and *Oxalis acetosella* established more readily from transplants introduced in the spring. Petersen and Philipp (2001) concluded that seed dispersal was potentially more effective than clonal growth in the spread of introduced ground flora species over 10 years in a 40 year old Danish beech plantation on former arable land. However, in practice, no significant difference was detected between the two modes of dispersal. The lack of dispersal agents, such as ants and the slow build-up of plant populations with abundant seed production were thought to be major factors limiting spread. However, the light and soil conditions in the beech plantation were believed to have been sub-optimal for many of the introduced species, half of which did not survive the 10-year experiment. It is notable that no pre- or post-establishment woodland management was carried out in this experiment.

Ground flora enhancement by seeding has the advantage of introducing greater genetic diversity than vegetative plant material. Cohn (1994) recommended a sowing rate of 100 seeds m^{-2} for species with relatively low germination and survival rates, such as *Primula vulgaris, Viola riviniana* and *Campanula trachelium* and a rate of 25 or 50 seeds m^{-2} for the more ubiquitous *Silene dioica* and the woodland grasses, e.g. *Bromopsis ramosa* and *Milium effusum*. Cohn (1994) emphasised the importance of autecological knowledge coupled with observations of community behaviour in maximising the success of ground flora enhancement schemes and ensuring their practical and economic viability.

To date much of the research on ground flora enhancement has concentrated on the regulation of the light climate to permit growth of introduced species while inhibiting undesirable spontaneous species (e.g. Boorman, 1990; Fu and Buckley, 1991; Francis *et al.* 1992; Street and Mond, 1992). This usually involves ground flora introductions on canopy closure. However, vigorous spontaneous field layers often persist after canopy closure on fertile urban sites and the creation of suitable germination and establishment niches is likely to be vital. Buckley and Knight (1989) acknowledged that in such situations herbicides might be needed to eradicate invasive plants. Cohn (1994) and Cohn and Millet (1995) found the use of herbicides and mulches, separately or in combination, invaluable at initially eradicating or suppressing competitive spontaneous vegetation prior to seed introductions. Both Francis (1993) and Cohn (1994) stressed the importance of careful site selection, informed by survey, for ground flora enhancement schemes. Francis (1995) proposed the introduction of different functional groups of species according to canopy openness and the extent of spontaneous field layer vegetation. By contrast Cohn (1994) focused on tailoring ground pre-treatment to canopy and field layer type.

Although establishment environment is crucial for success of ground flora enhancement (Cohn, 1994), post-enhancement management is also vital for the persistence of target species and communities. This management must strike a balance between the maintenance of conditions suitable for the regeneration of the introduced flora and the control of competitive spontaneous vegetation which could prevent this (Cohn, 1994). To date there is little literature on this subject, suggesting that it would be helpful to monitor new schemes to assess success and inform future management. Cohn (1994) advocated targeted use of thinning and coppicing to manipulate canopy structure and therefore the light climate with the objective of competitively favouring the introductions over the aggressive and / or non-woodland species.

The literature on habitat reconstruction and woodland ecology suggest that major influences on field layer enhancement are likely to include light intensity and soil fertility. The remainder of the present literature review examines these influences and the possibility that their interaction has itself a profound influence on woodland habitat reconstruction via ground flora enhancement in secondary woodlands.

1.6 The influence of light intensity on woodland field layers

1.6.1 Light as an ecological factor

Light is usually the most limiting environmental factor for field layer herbs in woodlands (Packham *et al.* 1992). This is supported by Maranon and Bartolome (1993) who found, using reciprocal turf transplants between Californian oak woodland and adjacent grassland, that light-demanding grassland species were eliminated within two years under woodland light conditions. They also reported that shade-tolerant woodland species were out-competed by high seed-producing grass species in the open. The complex nature of the deciduous woodland light climate is described by Mitchell (1992). Light varies simultaneously in quantity and quality. Fluctuations are both temporal and spatial (conforming to seasonal and daily cycles). In the short term, and exhibiting seasonal trends, sunflecks (Chazdon, 1988) can strongly influence irradiance patterns at the level of the herb microclimate. Spectral variations in time and space are reported by Endler (1993). The red to far-red ratio is known to be important in plant growth (e.g. Dudley and Schmitt, 1995) and workers such as Mitchell and Woodward (1988) have investigated its influence on woodland ground flora species. Mitchell and Woodward (1988) found that the percentage transmission of PAR affected plant growth and that the red to far red ratio influenced leaf architecture, allowing plants to maximise light interception, in factorial experiments on *Cirsium palustre, Lamiastrum galeobdolon* and *Sanicula europaea*. Martens *et al.* (2000) modeled the understorey light climate across a grassland / forest continuum and stated that spatial variation in the understorey light climate is determined largely by the distribution, height and cover of the canopy plants. Grime and Jeffrey (1965) highlighted the importance and timing of vertical light gradients to field layer plants. Naumburg and De Wald (1999) found that graminoid field layer diversity under Ponderosa pine was correlated with basal tree diameter (larger trees produce less dense shade), whereas graminoid abundance and density was related to direct sunlight.

Light intensity and quality influence the development of field layer vegetation. Plant responses to changes in light regime are both physiological (i.e. a measure of photosynthetic efficiency) and morphological (i.e. a measure of relative tissue allocation to organs). Light adaptations can be both by genetic adaptation and by phenotypic plasticity as Packham and Willis (1976); Boardman (1977); Corre (1983a,b) have reported for sun and shade plants. Corre (1983a,b) concluded that responses of sun and shade plants to the woodland light climate depend on light quality and not light intensity.

However, Fitter and Ashmore (1974) suggested that shade-tolerance in *Veronica montana* involves adaptations to both low light intensity and enhanced far-red light stresses. *Lamiastrum galeobdolon* showed phenotypic plasticity in response to variations in the light climate by production of sun and shade leaves (Packham and Willis, 1982). *Silene dioica* also exhibits sun and shade adaptations (Willmot and Moore, 1973), and takes about 18 hours for photosynthetic shade adaptation to occur in the field (McKiernan and Baker, 1992). Pitelka and Curtis (1986) found that the light climate at establishment dictated whether plants of the understorey herb, *Aster acuminatus*, became sun or shade plants. Hutchinson (1967) found that establishment light climate affected a plant's ability to withstand prolonged periods of darkness.

Murchie and Horton (1997) demonstrated the continuum of potential for light acclimation of photosynthesis in 22 British plant species and demonstrated the link with species habitat distribution. Murchie and Horton (1997) suggested that inter-species variation could be explained by the presence of two acclimation strategies, one at the leaf level (altering leaf chlorophyll content) and the other at the chloroplast level (altering relative amounts of the photosynthetic pigments). These strategies are of most importance to plants in intermediate light climates where phenotypic plasticity is likely to be essential to competitive success; whereas, truly shade tolerant plants do not employ these strategies. Verburg and During (1998) demonstrated the plastic response of *Circaea lutetiana* in its phenology to varying light regimes; and also demonstrated the limitations of this response, with no effect found in reproductive resource allocation. Salisbury (1976) highlighted the importance of vegetative spread in woodland herbs, to compensate for low seed production in shaded conditions. However, Bierzychudek (1982) found, in a phenological and demographic review of shade-tolerant temperate forest herbs, that most species were able to reproduce by seed. Petersen and Philipp (2001) found that vegetative spread was no more important than seed dispersal in an introduced ground flora under a high-shade beech canopy. Pons (1977b) showed that *Geum urbanum* exhibits plasticity in its shade tolerance throughout the coppice cycle. Genotypic variability of *Brachypodium sylvaticum* was demonstrated by Davies and Long (1991) under differing shade regimes. Dudley and Schmitt (1995) suggested that adaptive evolution could be responsible for differing photo-morphogenic responses in populations of *Impatiens capensis* from open and woodland sites.

Variations in woodland light climate creates variable niche space within the habitat. Successful niche colonisation and consolidation can be influenced by light regime. For example, Valverde and Silvertown (1995) reported that *Primula vulgaris* fecundity was positively correlated with light. Dzwonko (2001) showed that the colonisation pattern of a pine plantation by species from a nearby ancient semi-natural woodland was affected by light intensity; and that response depended on plant functional groups. Light intensity was positively associated with colonisation by non-woodland and wind dispersed species (anemochores). Reader and Bricker (1994) demonstrated that thinning increases irradiance and the exposure of bare mineral soil, both of which encouraged invasion by undesirable non-forest species. They concluded that only minimal thinning (e.g. 33% removal of tree basal-area from a 0.01 ha plot) would be compatible with conservation objectives within deciduous forest nature reserves. Buckley *et al.* (1997b) demonstrated the importance of ride edge management to replenish the soil seed bank in under-managed woodlands.

Silvicultural treatments which manipulate the tree canopy influence irradiance reaching the woodland floor, with subsequent effects on the composition and growth of ground flora communities. Such effects have been reported by Reader and Bricker (1991) after canopy thinning, by Ford and Newbould (1977) and Pons (1977a,b) following coppicing, and by Sparks *et al.* (1996) and Buckley *et al.* (1997a) after ride clearance.

Buckley *et al.* (1997a) reported enhanced ground flora response following ride clearance, but also a shift towards a perennial non-woodland flora. Falkengren-Grerup and Tyler (1991) found that woodland herbs such as *Oxalis acetosella, Lamiastrum galeobdolon* and *Melica uniflora* were sensitive to heavy thinning, but that others, including *Milium effusum* and *Stellaria nemorum* (and species associated with open habitats, e.g. *Urtica dioica, Galeopsis tetrahit*) were favoured by thinning. Kirby (1990) compared the effects of thinning, coppicing and clear felling on woodland ground flora at a single site in Buckinghamshire. Felling or coppicing led to an initial shift from stress-tolerant ground flora species to competitive and ruderal species. This shift was most marked on clear fell sites, whose subsequent decline in species-richness was greater than in coppice blocks. Coppicing seemed to favour later dominance by *Rubus fruticosus* agg., whereas clear-fell favoured dominance by grasses. Humphrey (1996) discussed the effects of thinning, fencing (i.e. excluding deer grazing) and planting position on introduced ground flora (dwarf shrub) species in a Scottish pine plantation. Humphrey (1996) found that the

survival, growth and spread of most species were favoured by grazing exclusion and that increased irradiance improved the success of *Empetrum nigrum* and *Vaccinium* species due to thinning and planting position, respectively.

Tree canopy species will affect the light climate, the amount and type of litter produced (Graae and Heskjaer, 1997) and water budgets (Price and Watters, 1989). Tree canopy species can be seen as a product of past silvicultural management. Kirby (1988) described varying ground flora diversity under different species canopies of various age, both plantation and semi-natural. Kirby (1988) found that field layer diversity was greater in semi-natural oak stands, pine plantations and some conifer-broadleaf mixtures than under beech, Norway spruce and Lawson cypress stands of similar age. Graae and Heskjaer (1997) reported differences in field layer vegetation between managed and unmanaged deciduous forests in Denmark. Graae and Heskjaer (1997) found that differences in canopy composition were more important than management effects on stand structure. The only significant difference associated with management was the greater proportion of species characteristic of wet conditions in the unmanaged forests.

Barkham (1992) reported no long-term effect of silvicultural treatment on ancient woodland species. This is supported by Kirby (1988) who showed that field layer diversity increased after clear felling, declined during the thicket stage and subsequently increased on thinning. This pattern was also observed by Ford and Newbould (1977) in the ground flora biomass during a coppice rotation in south-east England. This also fits with the adaptive phenology of *Digitalis purpurea*, which alters its reproductive strategy to allow persistence throughout the forest cycle (van Baalen and Prins, 1983).

1.6.2 Measurement of the woodland light climate and ground flora response

Quantification of ground flora response to light intensity can be measured either at the species level, both in the field (e.g. Buckley *et al.* 1997a) and under simulated woodland light conditions (e.g. Fitter and Ashmore, 1974), or at the community level (e.g. Barkham, 1992). While autecological data shows species response either in isolation or in very simple mixtures (to incorporate competition effects) and is invaluable when composing a seed mix (Cohn, 1994), it gives only limited insight into community response.

Quantification of the complex woodland light climate has been attempted by many workers (e.g. Anderson, 1964a,b, 1966; Evans, 1966). While it is photosynthetically active radiation (PAR, 400-700 nm) that herbs are responding to, direct measurements within a woodland become almost meaningless when spatial and temporal variations are taken into account. Fluctuations are so great that comparisons through time or across space are not viable; only simultaneous readings can be compared (e.g. Musgrove, 1998). Reader and Bricker (1994) employed a 'light quadrat', where irradiance was measured, with a quantum sensor, at each corner of the quadrat, at a height of 1 m above the ground. Tube solarimeters are useful at averaging horizontal spatial variation in herbaceous crops (Cannell and Grace, 1993), but are unsuitable for use in urban woodlands, prone to vandalism. Vertical variations in light interception, the importance of which in woodlands was highlighted by Grime and Jeffrey (1965), has been estimated within a crop canopy using point quadrats (Wilson, 1965). Continuous measurement can give a useful indication of change in light intensity with time (e.g. Rich *et al.* 1993), but this is unsuitable when applied to the spatial and temporal scales of the current research. PAR reaching the woodland floor is usually expressed as a percentage of ambient levels (e.g. Mitchell and Woodward, 1988). Mitchell and Woodward (1988) found that absolute PAR levels and the timing and duration of sunflecks were more important than light quality (the red to far-red ratio), which was found to have had little or no effect on the growth responses of three British woodland herbs. Light intensity can be measured chemically, e.g. by the anthracene-benzene technique (Perkins *et al.*, 1987), which uses the polymerisation of anthracene to dianthracene by ultraviolet light. However, such methods may not produce results directly comparable to PAR. Bioassay, or the use of primary productivity, as an approximation of light interception (Cannell and Grace, 1993), is destructive and perhaps more suited to studies of tree crop production than investigations of ground flora response. Cannell and Grace (1993) reviewed both indirect and direct methods of measuring the woodland light climate.

Many workers have found that hemispherical photography provides a useful indicator of woodland floor light climate, and facilitates comparisons in time or space (e.g. Holbo *et al.*, 1985). Anderson (1966) asserted that direct sunlight can only be measured using hemispherical photography, which provides an acceptance angle of 180° and therefore overcomes the problems of leaf incidence angle and the effects this will have on future light pathways (i.e. reflection, transmission) and spectral type, within the canopy. Hemispherical photography in woodlands has been used throughout the 20th Century.

The manual analysis of these photographs became more complicated with the development of increasingly complex mathematics, which allowed description of different aspects of the light climate. Evans (1966) and Evans *et al.* (1966) reviewed advances in this field. Analysis of a hemispherical photograph involves the superimposition of solar tracks and a grid which divides the image into concentric angular zones (Anderson, 1964a). Differentiation between shaded and unshaded zones allows calculation of the gap fraction and leaf area index (Cannell and Grace, 1993). Barrie *et al.* (1990) developed a semi-automated method for faster analysis of hemispherical photographs, however, the advent of digital technology has allowed rapid computerised analysis of photographs using software such as SOLARCALC (Chazdon and Field, 1987) or HemiView canopy analysis software (Delta-T Devices Ltd., 1998, 1999). This method is only really limited by the quality of the photograph, e.g. still, dull, over-cast conditions are required to maximise shade differentiation, and high-resolution images are required at the point of electronic capture. The shade percentages determined can be usefully compared across stands, sites and seasons. However, this information is relative and knowledge of any relationship with actual PAR readings is useful (Section 6.7). Rich *et al.* (1993) used long-term continuous direct monitoring of PPFD (photosynthetic photon flux density) to calibrate hemispherical photography, permitting reliable estimation of PPFD using this technique. The tropical forest light climate quantified by Rich *et al.* (1993) is overall far more uniform than that of temperate deciduous woodlands, e.g. sun-flecks are likely to be large in size and duration compared to the small, low-intensity, rapidly-changing sunflecks characteristic of tropical forests (Coombe, 1966). Chazdon (1988) asserted that photosynthetic utilisation of sunflecks by understorey plants is likely to be more efficient during brief, but frequent, low intensity sunflecks.

In conclusion, the methodology used for measurement of the complex woodland light climate will depend on the aspect of the light climate being investigated. From the literature, PAR reaching the ground flora plants (i.e. measured at the top of the ground flora canopy) appears to be the most important factor influencing growth response. Quantification of the spectral quality of light (e.g. the red to far-red ratio) appears to be less important than measuring irradiance in the form plants respond to (i.e. PAR). As continuous measurement is not practicable in urban situations, prone to vandalism, paired simultaneous readings (expressing PAR within the woodland as a percentage of ambient levels) appear to provide a relatively robust measurement of irradiance reaching the

woodland floor. Such readings can be directly related to hemispherical canopy photography (Section 6.5).

1.7 The influence of soil fertility on woodland field layers

1.7.1 Woodland soils

Ancient woodland soils are relatively undisturbed with a definable structure. Typical characteristics of such soils are described in Packham *et al.* (1992). Rodwell (1991) described soils of the W8 (*Fraxinus excelsior – Acer campestre – Mercurialis perennis*) woodland target community. Intra-site edaphic variations range from sites with a relatively uniform soil type, like that of Hayley Wood (Martin and Pigott, 1975), to those with extremely complex and detailed soil patterns, such as the Wyre Forest (Oliver, 1994). Silvicultural practices influence these patterns and may lead to acidification of surface horizons (Peterken, 1993; Huttl and Schaaf, 1995). The effect of tree species (both coniferous and broad-leaved) on edaphic conditions is well documented, especially its influence on pH (e.g. Beniamino *et al.* 1991; Norden, 1994). Anderson (1987) questioned the importance of tree species effects over the longer term. However, Binkley and Valentine (1991) reported divergent biogeochemical conditions between stands of different species after 50 years of woodland development. Gilliam *et al.* (1995) suggested that disturbance caused by silvicultural practices may alter the balance between soil factors and stand characteristics as the major determinant of ground flora development. Forest soil ecosystems are not static, but in a constant state of flux. Attiwill and Adams (1993) and Nilsson *et al.* (1995) reviewed nutrient cycling in forests. Brown (1974) quantified nutrient cycling in an English oak wood. Farley and Fitter (1999a) described both spatial and temporal variation in macronutrients and pH over a two-year period in an English woodland soil (Section 1.7.6). Longer term changes in forest soils and their nutrient cycling systems have been reviewed by Johnson *et al.*, (1991) and research approaches are discussed by Powers and Van Cleve (1991). Bjornstad (1991) reported the effects of long-term edaphic changes on vegetation in Norwegian forests (Section 1.7.3.4).

In contrast to ancient woodland soils, soils of recent secondary woodlands tend to have poorly developed topsoil structure. They may have been ploughed and fertilised (e.g. Aarnio *et al.*, 1995; Burgess *et al.*, 1995) leading to short term fertility increase and the enhanced possibility of nutrient losses via leaching (e.g. Persson and Wiren, 1995). Fertilisation may also cause less predictable long-term effects, such as stimulating plant

cation uptake from deep in the soil profile (Turner and Lambert, 1986), making more nutrients available for cycling within reach of the field layer. Liming is also a common practice in acidified woodland systems. Kreutzer (1995) reviewed the effects of liming on woodland soil processes. Bauhus and Bartsch (1995) acknowledged the role of liming in buffering ecosystems to nutrient loss, and Alva *et al.* (1991) demonstrated that these effects are more pronounced in woodland soils than agricultural soils.

A consideration of urban woodland soils further complicates the situation, where topsoil may be absent, or in early phases of pedogenic development. Urban substrates are likely to vary greatly in the nature of their physical (Mullins, 1991) and chemical (Pulford, 1991) properties. Fertility levels may represent extremes at either end of the fertility spectrum. Urban soils frequently lack the organic matter and developed nutrient cycles characteristic of ancient woodland (Packham *et al.*, 1992). This may be exacerbated by vandalism, in the form of fire, which will remove organic matter from the system. Soil flora and fauna (including mycorrhizal associations) are likely to be less well developed in urban soils. The classification of urban soils is essentially undeveloped (Effland and Pouyat, 1997), and the process of 'anthropedogenesis' (human impact on soil formation) is poorly understood.

1.7.2 Plant mineral nutrition

Plants depend on the soil to provide the latter two of their three requirements: light, water and mineral ions. Therefore, soil conditions are likely to have a large influence on plant community composition and hence diversity. Soils are often characterised in terms of their fertility or productivity. Marrs (1993) defined soil fertility as "a function of the combined effects of all ecosystem processes which produce a supply of essential nutrients for plant uptake" and stated that soil fertility is most likely to be controlled by the three major macronutrients nitrogen, phosphorus and potassium. These essential macronutrients exist within the soil in four pools: mineral, organic matter, exchangeable / extractable and soil solution. The exchangeable / extractable pool and the soil solution contain nutrients in forms available to plants, however, pool size and fluxes between pools vary considerably and are difficult to define (Marrs, 1993).

1.7.2.1 Soil nitrogen

Nitrogen in soils occurs in both organic and mineral forms and is inherently mobile and unstable. Nitrogen is available to plants in two forms, nitrate (NO_3^-) and ammonium (NH_4^+), the former being more common in most soils. Most total nitrogen in soils is unavailable to plants and bound up in the humic fraction. The process of mineralisation releases some of this nitrogen for plant uptake. The mineralisation process is caused by microbial activity and depends on many factors, such as substrate chemistry, type of organic compound, pH, micro-faunal diversity, temperature, moisture, aeration and plant uptake (Pearcy *et al.*, 1991).

Mineralisable nitrogen is a measure of the size of the mineral fraction that is readily released by microbial activity and provides an indication of nitrogen availability (Dolmat *et al.*, 1980). Therefore, mineralisable nitrogen approximates to the amount of nitrogen available for plant uptake. This is supported by Kabzems and Klinka (1987), who found that mineralisable nitrogen explained the main variation in understorey vegetation. Anaerobic mineralisation has been used as a predictor of yield in agricultural systems which correlates with total nitrogen (Dolmat *et al.*, 1980). Nitrogen is known to be a controlling factor in community composition of semi-natural grasslands; the addition of which is associated with decreased plant diversity (e.g. Tilman, 1983; Gough and Marrs, 1990a,b). McCrea (1999) demonstrated a negative correlation between species diversity in grassland and mineralisable nitrogen.

Persson and Wiren (1995) described influences on nitrogen mineralisation in acidic forest soils in southern Sweden and eastern Denmark; these were soil pH and micro-biota, both of which varied with depth. Nitrogen mineralisation and nitrification are caused by temperature-dependent microbial activity, which varies with climate. In undisturbed temperate and boreal forests the rate of nitrogen mineralisation followed by plant uptake is estimated at between 5 kg and 100 kg pa (Attiwill and Adams, 1993). Nitrogen mineralisation is usually slower in the field than in the laboratory and slower in forest soils compared to agricultural soils. These slow rates of mineralisation in forest soils were often associated with poor nitrification (Attiwill and Adams, 1993). Castaldi and Smith (1998) found that woodland soil exhibited very low denitrification activity compared to arable soil on similar parent material.

Silvicultural treatment can affect nitrogen mineralisation. Kim *et al.* (1995) reported that even light thinning (leaving 75% canopy cover) of northern red oak stands in Michigan led to increased nitrogen mineralisation. Chang *et al.* (1997) found that inorganic nitrogen fertiliser was immobilised within hours by microbes in the humus layer, in a system with a large soil pool of mineral nitrogen, and that this nitrogen had low future mineralisation potential. Lambert *et al.* (1994) reported the effects of herbicide application and mulching, as measured by nitrate reductase activity. The effects of tree species on nitrogen mineralisation have been reported in primary and secondary woodland, including successional trends (Liu and Muller, 1993; Pare and Bergeron, 1996). Knoepp and Swank (1997) play down the long-term effects of silvicultural treatments on nitrogen cycling.

1.7.2.2 Soil phosphorus

Soil phosphorus occurs mostly in the form of phosphate and as with nitrogen, both organic and inorganic forms are significant. Phosphate release from weathering is very slow. Phosphates readily bind to soil surfaces and phosphorus availability is strongly influenced by soil particle type (Grime, 1979). Therefore, this nutrient is highly immobile and soluble soil phosphates quickly become unavailable to plants. This means that the soluble phosphate pool is small (Allen *et al.*, 1989) and that uptake by plant roots can lead to localised depletion and nutrient stress (Rowell, 1994).

Studies of forest nutrient cycling in the temperate Northern Hemisphere have largely focused on nitrogen as a limiting factor; however, it seems likely that phosphorus may be limiting in many ancient forest soils. There is increasing evidence to suggest that phosphorus is immobilised more readily in the first stages of litter decomposition than nitrogen and in some forests active phosphorus cycling is confined to the litter layer (Attiwill and Adams, 1993).

Chemical techniques for measuring available phosphorus tend to be more efficient than plant roots at extracting all of the available phosphate into solution, and therefore tend to overestimate the amount available to plants (Rowell, 1994). Enzyme activity can influence the rate of phosphorus mineralisation (Joner *et al.*, 2000). Vaz (2001) investigated the role of phosphatase in influencing semi-natural grassland diversity and found that soil phosphatase activity was higher in diverse semi-natural grasslands compared with newly created grassland on arable soil. Vaz (2001) suggested that it may

take more than a year in grassland restoration schemes to develop a soil microflora capable of controlling nutrient cycling. Soil phosphate concentrations are known to play an important role in influencing grassland community composition (Bradshaw *et al.*, 1960). As with nitrogen, the addition of phosphate is associated with a decline in plant diversity in semi-natural grasslands. High residual phosphates in agricultural soils are a major barrier to the restoration or creation of species-rich grassland. Marrs (1993) reported that it might take over 70 years for soil mineral phosphorus levels in improved grassland to return to those comparable with that of semi-natural grasslands. McCrea (1999) proposed 70 mg kg^{-1} available phosphorus as an upper limit for the successful creation of species-rich grassland.

1.7.2.3 Soil potassium

Potassium does not form organic compounds and occurs only in the inorganic soil fraction (Jeffrey, 1987). Most soil mineral potassium is unavailable to plants and its release by weathering is slow. Total soil potassium bears little relation to that available for plant uptake and is seldom measured in ecology (Pearcy *et al.*, 1991). Measurement of available potassium is undertaken via extraction techniques, which, as with phosphorus, tend to overestimate the amount likely to be taken up by plants (Rowell, 1994).

The relationship between potassium and species diversity is less well understood than that of nitrogen and phosphorus. A humpback relationship (Grime, 1979) is suggested by McCrea (1999) and McCrea *et al.* (2001b), in which both very low (< 100 mg kg^{-1}) and high (> 400 mg kg^{-1}) concentrations of available potassium prohibit diversity in grassland systems. Although many workers have measured available soil phosphorus and potassium in woodlands (e.g. Farmer (1995) at Wytham Wood, Oxfordshire), few have studied implications for the field layer. While Fitter and Setters (1988) showed varying phosphorus and potassium allocation patterns in six species of *Viola* at 10 Yorkshire sites (Section 1.7.7), few studies have identified these soil factors as major determinants of woodland ground flora development. Available potassium has been identified as a trigger factor causing a shift from one field layer community to another in a modeling study of a small urban secondary woodland with an introduced ground flora in the West Midlands (Hooley and Cohn, in prep).

Availability of nitrogen, phosphorus and potassium is affected in different ways by pH, soil moisture (Rorison, 1987), soil physical properties and soil flora and fauna. These factors interact, producing complex effects on soil fertility (Crawley, 1997). Factors influencing soil fertility are reviewed by McCrea (1999) and Vaz (2001).

1.7.3 Soil physical characteristics

1.7.3.1 Soil structure

Soil structure is dependent on parent rock type and weathering rate (Jeffrey, 1987). The solid soil fraction is usually aggregated into peds. Ped size and type affects porosity and therefore aeration and drainage. The movement of air and water through soil influences biological activity and mineral nutrient availability to plants (Rowell, 1994). Silvicultural treatment can affect soil structure, e.g. the planting of conifers can lead to podzolization and structural breakdown (Grieve, 1978). Messing *et al.* (1997) demonstrated the effects of tree planting on arable land on soil physical properties, including enhanced aggregate stability, porosity and hydraulic conductivity. Soil texture (i.e. the relative particle size distribution of the soil fine-earth fraction) will influence nutrient input from weathering, nutrient transport, nutrient retention and leaching. For example, sandy soils have low nutrient or water holding capacity and a minimal nutrient supply from weathering, whereas clays can absorb water and retain nutrients for plant uptake. Clay soils have a relatively high cation-exchange capacity, i.e. they are able to hold cations, such as potassium, on their surfaces, and can provide a major soil pool of exchangeable cations.

1.7.3.2 Soil organic matter

Soil organic matter stabilises soil structure and influences fertility in several ways. The presence of organic matter in the soil increases cation-exchange capacity, lowers pH, and increases water and nutrient holding capacity, especially for nitrogen. Soil organic matter usually accumulates over time in undisturbed soils and plays an increasingly important role in community composition as succession proceeds (Marrs, 1993; Boerner *et al.*, 1998). Soil organic matter adds to soil heterogeneity, which leads to localised patches of nutrient enrichment, which in turn affects plant diversity (Fransen *et al.*, 1998).

1.7.3.3 Soil moisture

Soil moisture affects fertility by providing a transport mechanism for mineral nutrients and a pool of available nutrients in the soil solution. Water is essential for life and competition for this resource can be intense in a multi-layered woodland community where drought can limit the growth of ground flora plants. Waterlogging may also be a problem on some soils where drainage is impeded. Although woodland herbs tend to possess a stress tolerant strategy (Grime, 1979), they vary considerably in their tolerance of water stress. In an autecological study of three woodland annuals, Cid-Benevento and Werner (1986) found light intensity, rather than soil moisture, to be the driver of fecundity. However, DeMarrs and Runkle (1992) found soil moisture to be the major determinant (after age since abandonment) of ground flora development during secondary woodland succession. Farley and Fitter (1999a) found soil moisture remained relatively constant over a two-year sampling period in an ancient deciduous woodland in North Yorkshire.

1.7.3.4 Soil pH and acidification

Although soil pH may inhibit root growth in acidic soils (e.g. in *Deschampsia flexuosa* (Balsberg-Pahlsson, 1995)), the most major indirect influence of pH on plant distribution is its effect on nutrient availability. At low pH, microbial activity is inhibited and cations are leached into solution. In acidic soils the availability of phosphate, nitrate and sulphate is enhanced, whereas mineral nitrogen is more likely to occur in its ammonium form, as acidity inhibits nitrification (Vaz, 2001). Different plant species display varying tolerance to extremes of pH. Marrs (1993) believed that this direct effect of pH largely dictates community composition in English grasslands, whereby neutral and basic soils support greater diversity, as more grassland species can tolerate these pH conditions than acidic ones. However, this is not the case in woodlands, where acidic soils can be associated with high field layer diversity. Soil pH usually decreases with succession in woodland soils and was found to be a major determinant of ground flora development in secondary woodlands in Hertfordshire (Harmer *et al.*, 2001) and Belgium (Verheyen and Hermy, 2001).

The effect of tree species on pH in broad-leaved woodlands is well documented (e.g. Beniamino *et al.*, 1991; Norden, 1994). As pH influences nutrient availability, it also has the potential to affect toxicity (Grime, 1979). Falkengren-Grerup and Tyler (1991) showed that increasing soil acidification in Swedish beech forests was accompanied by

increasing solubility of toxic elements. This is supported by Luwe (1995), who concluded that element uptake, including heavy metals, by field layer plants is indirectly controlled by topsoil pH. Falkengren-Grerup and Tyler (1991) also reported increased nitrogen deposition over the 10-year study period. They cited long-term soil acidification as the major determinant of ground flora development, which served to exclude the more calcicolous woodland species, such as *Galium odoratum, Viola riviniana* and *Mercurialis perennis*.

Soil acidification decreases cation exchange capacity (Stanturf and Stone, 1994), affecting cation availability for plant uptake. However, Falkengren-Grerup (1995) demonstrated, via fertilisation of transplanted field layer species, that it was the direct effect of low pH, and not potassium, calcium or magnesium limitation, which determined ground flora species response. Bjornstad (1991) found that the major effects on the field layer vegetation in contrasting forest soils in southern Norway were the long-term build-up of organic matter and soil acidification with its consequences for nutrient availability, which was partly countered by increased cation deposition from the North Sea. Martin (1968) demonstrated an interaction between waterlogging and iron toxicity in woodland herbs. Although pH influences soil fertility, Ellenberg (1988) demonstrated, with woodland herbs under experimental conditions, that pH does not affect plant growth when nitrogen is not limiting.

When studying nutrient cycling, consideration must also be given to acidic atmospheric deposition. Falkengren-Grerup and Eriksson (1990) found that long-term nitrogen deposition had been a major determinant of ground flora development in Swedish beech forests. De Vries *et al.* (1995) described the main impacts of sulphuric and nitrogenous deposition on acidic forest soils in The Netherlands, including an increase in aluminium leaching. Gilliam *et al.* (1994) found little short-term response of field layer plants to induced acidification, but concluded that future toxicity problems are likely with the increased mobility of aluminium and micronutrients. Farmer (1995) quantified long-term nitrogen deposition in Wytham Wood, Oxfordshire. Crabtree and Bazzaz (1993) concluded that chronic nitrogen deposition alters the form and quantity of available nitrogen, which affects plant shade tolerance at the species level with consequences for light-mediated competition. Johnson *et al.* (1997) showed that elevated atmospheric carbon dioxide increased plant growth and nutrient uptake, which has implications for the sustainability of nutrient budgets in commercial forests.

1.7.4 Soil microbiota

The soil micro-organisms, which are largely responsible for the decomposition of soil organic matter and the mineralisation of nutrients, consist of algae, protozoa, fungi and bacteria. The root-soil interface (rhizosphere) tends to be colonised by bacteria and fungi. Certain groups of these bacteria (root nodule bacteria) and fungi (mycorrhizae) directly infect the root, facilitating plant nutrient uptake without harming the plant (Garrett, 1981). Symbiotic relationships between plants and mycorrhizae (particularly vesicular-arbuscular mycorrhizae, which are widespread in most angiosperm families) are thought to have a positive influence on diversity in semi-natural ecosystems (Read, 1998). Mycorrhizae predominately enhance phosphate acquisition (e.g. Merryweather and Fitter (1995a,b); Hodge *et al.*, 2000) and influence nitrate and ammonium uptake (Ozinga *et al.*, 1997; Hodge *et al.*, 1998). Most forbs form mycorrhizal associations in the field and certain species, e.g. *Hyacinthoides non-scripta*, are known to be obligate mycorrhizal symbionts (Merryweather and Fitter, 1995b, 1996). However, Merryweather and Fitter (1995b) suggested that *Hyacinthoides non-scripta* seedlings change from facultative to obligate symbionts (with respect to phosphorus nutrition) during approximately their first five seasons. This may have implications for ground flora enhancement using this species. Different species of mycorrhiza are known to have different functional properties. Therefore, mycorrhizal species diversity, as well as levels of infection, is likely to have an impact on plant species diversity. Clapp *et al.*, (1995) and Merryweather and Fitter (1998a) described the mycorrhizal diversity associated with *Hyacinthoides non-scripta* in the field. The mycorrhizal species colonising *Hyacinthoides non-scripta* roots in an English semi-natural woodland were shown to vary with season (Merryweather and Fitter, 1998b) and tree species (Helgason *et al.*, 1999). Whereas *Hyacinthoides non-scripta* is an obligate mycorrhizal species, *Silene dioica* is unusual in that it forms no known associations (Merryweather, pers. comm., 2001). This may have implications for ground flora enhancement on impoverished urban substrates, which may be lacking in nutrients and mycorrhizae. Evidence from grassland ecosystems suggests that new woodland soils may have poorly developed mycorrhizal communities. In grassland ecosystems, ancient semi-natural habitats usually have a well-developed and diverse soil fauna with the fungal component being most important in decomposition pathways. In contrast, frequently disturbed arable (and improved grassland) soils tend to have an under-developed fungal flora with bacterial pathways dominating the decomposition subsystem (Bardgett *et al.*, 1996 and Bardgett and McAlister, 1999). Bentham *et al.* (1992) proposed the use of three soil microbiological

indices (soil dehydrogenase activity, soil adenosine triphosphate and ergosterol) in assessing site suitability for habitat restoration on reclaimed soils.

1.7.5 Soil-plant interactions

Plants do not interact with their environment without influencing it and they affect soil structure and chemistry. The presence of a tree canopy influences nutrient cycling patterns (Browaldh, 1995). Dahlgren *et al.* (1997) reported that trees created islands of enhanced fertility (with raised organic matter, nitrogen, available phosphorus and potassium) in a Californian oak woodland. Both canopy and understorey plants vary in their efficiency of nutrient uptake and use, which feed back into nutrient cycling patterns (van Breemen, 1995). These feedback loops vary with tree stand development (Miller, 1995) and, on a different scale, with the phenology of the ground flora plants. Aber *et al.* (1991) found that the resource use efficiency of the vegetation was a key factor in modeling nitrogen cycling in temperate forest systems.

Tree canopy species composition affects the amount and type of litter produced (e.g. Bockheim *et al.*, 1991), which influences nutrient mineralisation and pH (e.g. Gower and Son, 1992; Raulund-Rasmussen and Vejre, 1995) and therefore affects ground flora species composition (Graae and Heskjaer, 1997). This 'litter effect' is also true of the ground flora species. Jandl *et al.* (1997) reported the effects of *Allium ursinum* litter in altering meso- and micro-faunal diversity and accelerating organic matter mineralisation. Litter alters the physical and chemical environment directly and indirectly. Litter decomposition can release nutrients and phytotoxins into the soil. The physical effects of litter influences soil chemistry by modifying decomposer activity. Accumulated litter provides a physical barrier to seedling emergence (as well as to seeds reaching the soil surface) and intercepts light, reduces soil thermal amplitude and evaporation. Litter also intercepts rainfall and inhibits infiltration, causing drought stress (Facelli and Pickett, 1991). Litter production is also dependent on successional processes. Verheyen and Hermy (2001) found that litter started to accumulate where low soil pH combined with high shrub density in a secondary deciduous forest in Belgium. Dzwonko (2001) showed that litter quality was a factor in woodland species colonisation. Litter which rapidly decomposed and led to humus accumulation positively influenced colonisation. The spatial distribution of woodland litter influences microclimate and therefore the availability of suitable germination niches. Pouyat *et al.* (1997) found that urban forests exhibited higher rates of litter decomposition and nitrogen mineralisation than rural

forests, and suggested that higher soil temperatures, and higher levels of atmospheric nitrogenous deposition, were part of the cause.

1.7.6 Spatial and temporal variations in soil characteristics

Soil resources are not evenly distributed in space, or time, but are present in a heterogeneous resource environment, the heterogeneity of which is compounded by the feedback mechanisms caused by the plants themselves. Spatial heterogeneity of soil nutrients often reflects the spatial heterogeneity of organic matter deposition (Vaz, 2001). Facelli and Pickett (1991) acknowledged that heterogeneous litter distribution will influence plant community composition, via both direct and indirect competition effects; and concluded that litter tolerance by certain plant species is likely to be a major determinant of community composition. Nitrogen, phosphorus and potassium exhibit seasonal cycling (Powlson, 1993; Davy and Taylor, 1974; Veresoglou and Fitter, 1984, respectively) as well as longer-term successional trends (Parish and Bazzaz, 1982). Farley and Fitter (1999a) demonstrated unpredictable cycling of phosphate, nitrate, ammonium and pH levels in an English woodland soil. Nutrient limitation patterns are likely to be complex at the community level. Olff and Bakker (1991) believed that the elements controlling plant community nutrient limitation could switch over time in grassland ecosystems. The heterogeneous soil resource environment cannot, in isolation, explain diversity, the effects of which are complicated by interspecific competition (likely to be intense in a multi-layered woodland ecosystem) and niche colonisation, plus other stresses due to disturbance or light limitation.

Farley and Fitter (1999a) showed that nutrient heterogeneity in ancient woodland soil operates at several scales: over a range of about 2 m for soil phosphate, ammonium and nitrate, but over about 20 cm for available nitrogen in the soil solution. Even smaller scale variation was measured by Gottlein and Matzner (1997), who showed that the heterogeneity of the soil solution chemistry (including toxic elements) of a forest podzol was significant on the cm-scale, e.g. with gradients of > 0.5 pH units within 2 cm. This heterogeneity is likely to influence plant distribution at the scale of the woodland field layer. However, the limited duration of localised nutrient-rich patches found by Farley and Fitter (1999a) in the field (less than a month) probably limits any localised morphological specialisation exhibited by ground flora herbs.

1.7.7 Measurement of woodland soil fertility and ground flora response

Most research into woodland soil fertility response has concerned tree crop production (e.g. Lambert *et al.*, 1994; Munson *et al.*, 1995). Finn and Braekke (1995) found that while nitrogen and phosphorus limited *Pinus sylvestris* growth in a nutrient-poor bog ecosystem in south-east Norway, the field layer tended to be phosphorus limited. Autecological studies on relevant field layer species have investigated growth responses to manipulation of nutrient supply under artificial conditions. Examples include the work of Pigott (1971) on *Urtica dioica* and phosphate and Falkengren-Grerup and Lakkenborg-Kristensen (1994) on the contrasting nitrogen nutrition of field layer species from Swedish deciduous forests. Quist (1995) demonstrated the inability of *Galium odoratum* to recover from episodes of elevated hydrogen and aluminium (i.e. two weeks of pH < 4.0 and Al > 20 μM at pH < 4.2), which could be induced by soil acidification, when compared to *Lamiastrum galeobdolon*; and concluded that temporary extremes in the soil chemical environment are likely to be a determinant of field layer species composition. Brunet (1994) used chemical ranges found in forest soil solutions in demonstrating the likely importance of pH and aluminium toxicity to the distribution of two woodland grass species.

Field studies potentially involve environmental variables in greater number and range compared with greenhouse studies. Fitter and Setters (1988) demonstrated the wide range of phosphorus and potassium allocation patterns in six *Viola* species at 12 sites in one growing season. They found between-population differences to be as great as those between species, and suggested considerable phenotypic plasticity or the existence of ecotypic differences. Pregitzer and Barnes (1982) found that *Viola* species were indicative of high pH and total nitrogen levels in an upland forest in Michigan. Falkengren-Grerup and Tyler (1993) obtained comparable autecological results in field and greenhouse studies on the effect of soil pH on ground flora species. Nutrient uptake and retention by species such as *Brachypodium sylvaticum, Circaea lutetiana, Galium odoratum, Milium effusum* and *Stellaria holostea* was impeded by high soil acidity.

The heterogeneous nature of the field soil resource environment further complicates the study of ground flora responses to fertility. In an autecological experiment performed under glasshouse conditions, Farley and Fitter (1999b) investigated the below-ground response of seven co-occurring woodland herbaceous perennials to soil nutrient heterogeneity. These were *Ajuga reptans, Glechoma hederacea, Oxalis acetosella,*

Silene dioica, Stachys sylvatica, Veronica montana and Viola riviniana. All species, apart from *Oxalis acetosella* and *Viola riviniana,* responded positively (via a combination of greater root proliferation, branching and elongation) to nutrient-rich patches. *Silene dioica* and *Veronica montana* were sensitive to nutrient concentration and *Glechoma hederacea* was sensitive to patch size. This evidence is supported by the work of Wijesinghe and Hutchings (1999), who showed that *Glechoma hederacea* was capable of localised morphological specialisation to enhance nutrient capture in all but the smallest and most contrasting nutrient patches. Farley and Fitter (1999b) also demonstrated that mycorrhizal colonisation had little effect on nutrient acquisition.

While autecological studies provide useful information, they cannot account for interspecific competition, the effects of which interact with soil fertility and other site factors. For example, in grassland systems Wilson and Tilman (1995) found that competitive effects tended to shift from roots to shoots as fertility increased, and to decline with increasing disturbance. Wijesinghe and Hutchings (1999) found that root : shoot ratios of *Glechoma hederacea* rose in nutrient rich patches as patch contrast (size and concentration) increased.

Hawkes *et al.* (1997) attempted to overcome the above problems of measuring the complex soil environment and the ground flora response to it. They used abundance-weighted Ellenberg indicator values of the vegetation in British forests, as a proxy bioassay. They found that mineralisable nitrogen and pH, as represented by mean N (soil nitrogen) and R (soil reaction) indicator values, provided an effective measure of soil fertility. Although the success of this pilot study was promising, more data across a wider range of conditions, using the 'British' Ellenberg indicator values (Hill *et al.*, 1999), will be required before chemical soil analysis becomes redundant. Meerts (1997) used foliar macronutrient concentrations of ground flora plants, in west European forests, to investigate the usefulness of Ellenberg's indicator values in elucidating soil conditions. Meerts (1997) found that foliar nutrient concentrations of nitrogen and phosphorus matched the availability of these nutrients in the soil, but that this was not the case for potassium. The mineral nutrient content of the forbs was more strongly correlated with the Ellenberg values than those of the graminoids. For the forbs, the N index allowed best prediction of nitrogen and phosphorus foliar concentrations, and the R index was positively correlated with potassium concentrations.

In investigating the woodland ground flora response to soil fertility there seems to be no non-destructive alternative to measuring soil fertility in the field. The literature suggests that measurement of the three main macronutrients in forms available for plant uptake (i.e. mineralisable nitrogen, extractable phosphorus and potassium) will provide a reasonable estimate of soil fertility. The influence of pH on the potential availability of these macronutrients makes its measurement essential. In woodland ecosystems the importance of the decomposition of the litter layer to nutrient availability cannot be underestimated (Attiwill and Adams, 1993). The percentage of topsoil organic matter gives an indication of the level of litter decomposition and therefore mineralisation of nitrogen and phosphorus. Soil organic matter influences pH, soil moisture and nutrient transport and its measurement is therefore invaluable in determining soil fertility.

To date, few studies have investigated the effects of soil fertility manipulation on field layer vegetation, either spontaneous (e.g. Kellner and Marshagen, 1991) or introduced (e.g. Braziotis and Papanastasis, 1995). Judgements about ground flora diversity in relation to soil fertility are therefore difficult to make. In addition, supporting evidence for relationships between soil fertility and diversity such as that predicted by Grime's (1979) humpback model have been demonstrated more in grassland (e.g. Jones *et al.*, 1990; McCrea, 1999; Vaz, 2001) than in woodland habitats. In broad-leaved woodlands the additional stress of shade complicates vegetation response. Petersen and Philipp (2001) found that unfavourable soil and light conditions caused localised extinctions in an introduced woodland ground flora in secondary woodland on former arable land. There is clearly a need for information on the interaction of these two environmental factors with respect to woodland ground flora.

1.8 The influence of soil fertility and light on woodland field layers

Slade and Hutchings (1987) reported that the phenotypically plastic responses of *Glechoma hederacea* to both light and nutrient stresses are similar. They do not, however, consider response to an interaction between the two factors. To date, there have been very few investigations which concentrated on the interaction between soil fertility and light intensity, and those that have with respect to woodland ground flora (e.g. Peace and Grubb, 1982; Dale and Causton, 1992) have largely been autecological. However, such information often serves to illustrate the complex nature of this interaction. For example, Ellenberg (1988) found that *Stellaria holostea* under field conditions needed 10 times the amount of light to enable it to grow on very acidic soils

where nitrogen availability was drastically reduced, compared with neutral soils, and concluded that minimal irradiance requirement increases with pH-related nutrient stress. In a multifactorial experiment involving manipulation of soil fertility and light intensity, Powelson and Lieffers (1992) found that *Calamagrostis canadensis* from forest populations produced a positive growth response to nutrient availability only when light intensity exceeded moderate levels. Braziotis and Papanastasis (1995) manipulated soil fertility and light intensity in a pine plantation undersown with the competitive non-woodland grass *Dactylis glomerata*. The introduced field layer responded most favourably to high levels of light and fertility and an absence of grazing disturbance.

Hogbom (1994) found that light climate had a considerable influence on the nitrate nutrition (via increased nitrate reductase activity) of ground flora species in Swedish beech forests. This is supported by Pitelka and Curtis (1986), who demonstrated that photosynthetic rates in the understorey herb, *Aster acuminatus*, were positively correlated with leaf nitrogen levels. In a study of the shade tolerant herb *Impatiens parviflora,* Peace and Grubb (1982) reported positive growth response to nitrogen and phosphorus at both extremes of the irradiance continuum. This contrasts with evidence gained by Blackman and Rutter (1947, 1948) for the sun plant *Hyacinthoides non-scripta,* or by Pigott and Taylor (1964) and Pigott (1971) for the moderately shade tolerant herb *Urtica dioica,* where significant nutrient induced responses were only found at high irradiance levels. However, this does not necessarily imply that such species of open habitats cannot persist under relatively dense canopies if nutrient levels are sufficiently high. The interaction between light and soil fertility also affects species response in the tree and shrub layers (Diekmann, 1996; Grubb *et al.*, 1996, respectively), accelerating canopy development with implications for field layer vegetation.

Chapin *et al.* (1987) believed that availability of more than one environmental resource below limitation thresholds would allow plants to benefit from the addition of any of these resources, by encouraging efficient physiological investment in resource acquisition. Cohn (1994) showed that the target species *Silene dioica, Circaea lutetiana* and *Viola riviniana* all responded positively to nutrient additions when light was limiting, and to irradiance increase when mineral nutrient supply was limiting. The exception was *Circaea lutetiana,* which did not show a significant increase in the latter situation within the time scale of the experiment.

The phenotypic plasticity and 'weed-like' strategy of *Silene dioica* allows it to occupy various habitats (Matlack, 1987). Slade and Causton (1979) found that *Silene dioica* and *Milium effusum* were able to germinate over a wide variety of conditions, but that *Circaea lutetiana* exhibited highly specific germination requirements under laboratory conditions. This evidence suggests the breadth of environmental adaptation achieved by woodland herbs and indicates their ability to successfully exploit a range of woodland conditions. Conversely, the non-woodland species are less able to exploit the full range of woodland conditions, but may be at a competitive advantage in certain situations. Brunet *et al.* (1997) suggested that pH was the major determinant of field layer plant distribution in Swedish oak forests, but that management-induced changes in light climate were responsible for short-term successional effects, where non-woodland and non-shade-tolerant woodland species gained a temporary competitive advantage. Gilliam *et al.* (1995) suggested that disturbance caused by silvicultural practices may alter the balance between soil factors and stand characteristics in determining ground flora development. Dzwonko and Gawronski (1994) found that field layer development in secondary woodlands, adjacent to ancient semi-natural woodlands, was more dependent on soil conditions, light climate and the influence of dominants than on the modes of species dispersal. This accords with the findings of Petersen and Philipp (2001) who found that regenerative strategy was not significant in the development of an introduced ground flora in secondary woodland on former arable land, but that favourable soil, light and moisture conditions were critical for plant survival.

Cohn (1994) suggested that woodland field layer vegetation is strongly influenced by the interaction between soil fertility and light intensity and that this is likely to be most evident during the establishment phase. Thus, an understanding of this interaction is crucial to the creation and management of woodland field layer communities representative of ancient semi-natural woodland. In attempting to understand this interaction, the influence of these factors on vegetation must be examined singly and in combination.

1.9 Contribution to knowledge of the current research

To date, information on vegetation response to the interaction between soil fertility and light intensity at the community level is lacking. This information is clearly needed to optimise woodland conditions for target species and to avoid situations where undesirable species are favoured and the vegetation shifts away from the target community (Section

1.4.1). The present study investigates the interaction at the community level via observation in secondary woodlands and experimentation with vegetation. The work has relevance for both habitat creation and the management of ancient and secondary woodlands and will aid prediction of the success of colonisation by woodland herbs and the course of succession in secondary woodlands.

1.10 Aims and objectives

The objective of the study was to experimentally investigate the field layer plant communities that develop following species introductions in secondary deciduous woodlands in relation to variations in soil fertility and light regime, manipulated by site management.

The central aims of the investigation were to:

- Test the hypothesis that in combination and in interaction, soil fertility and light intensity are major determinants of field layer development in urban secondary woodlands.
- Define ranges of soil fertility and light intensity, which in combination, optimise field layer development in the direction of desirable communities.
- Develop a model for the interaction between soil fertility and light intensity, with the aim of contributing to methodology for the creation of new woodlands with nature conservation value and the management of existing secondary woodlands for nature conservation purposes.

The investigation was based on a series of inter-related field and greenhouse replicated plot, single and multiple factor experiments. The experiments involved experimental manipulation and monitoring of soil fertility and light intensity in seeded plots. Soil fertility and light intensity were manipulated individually and in combination, in different experiments. The experiments involved monitoring species establishment in terms of cover, density (and height, biomass and leaf area in the greenhouse experiment) and the early development of the plant community.

1.11 Summary of experimental programme

Experiment 1: The light manipulation experiment at the Wolverhampton Environment Centre.

Experiment 1 investigated the influence of light regime on the establishment of ground flora communities within a simple secondary woodland. Manipulation of light climate was achieved by selective canopy thinning.

Experiment 2: The soil fertility and light manipulation experiment at Nedge Hill.

Experiment 2 investigated the effects of soil fertility and light regime in combination (including any interaction between the two factors) on field layer development in the establishment phase within a more complex (in terms of species composition, structure and development) secondary woodland. Tree thinning and fertiliser addition provided the means for manipulating the two environmental variables experimentally.

Experiment 3: The soil fertility and light manipulation experiment at the Plant and Environment Research Unit.

Experiment 3 investigated the effects of soil fertility and light regime in combination (including interactions) on ground flora establishment in completely artificial communities created within soil boxes. Soil fertility was manipulated by fertiliser additions at varying concentrations. Various grades of shade netting permitted manipulation of light intensity and quality within the artificial greenhouse environment. Experimental design, coupled with the artificial greenhouse environment within the polytunnel, allowed the control and / or statistical elimination of other potential environmental influences on the vegetation.

Chapter 2: Sites, Materials and Methods

2.1 Experimental programme

The investigation was based on a series of complementary field and greenhouse replicated plot, single and multiple factor experiments. The experiments involved experimental manipulation and monitoring of light intensity and soil fertility (manipulated individually and in combination) in seeded plots. All experiments were uniformly sown with a standard seed mix (Section 2.3). Where practicable, winter sowing was carried out to ensure natural vernalisation of seed (sowing dates are given in Table 2.1). The vegetation survey (Section 2.5) was designed to monitor species establishment in terms of plant cover, density (plus height, biomass and leaf area in Experiment 3) and the early development of the plant community. Environmental monitoring of the light climate (Section 2.4) and soil environment (Section 2.6) was undertaken to aid description of baseline conditions, elucidate treatment effects and to identify influences on the vegetation. The same establishment, measurement and analysis techniques have been used, as far as possible, throughout the experimental programme. Only generic methods are dealt with in this chapter; the establishment methods of each experiment are given in the relevant chapters (Sections 3.2.1, 4.2.1 and 5.2.1 for Experiments 1, 2 and 3, respectively), as are any deviations from the generic monitoring and analysis techniques. The experimental programme is summarised in Section 1.11.

2.1.1 Light treatments

Two standard light treatments were employed in the field Experiments 1 and 2. Selective canopy thinning was carried out to leave 50% of current cover and 100% as a control. These treatments were deemed to be practicable in terms of replication across plots and sites (by various operators) and by way of providing contrasting light climates, designed to initiate divergence in ground flora response. These standard field light treatments were arrived at after discussion with foresters and woodland managers. The experimental ground flora communities of Experiment 3 were subjected to three light treatments approximating to 30%, 20% and 5% of ambient Photosynthetically Active Radiation (PAR) provided by horticultural shade netting. These three treatments were designed to mimic the range of light conditions found in the field experiments.

2.1.2 Fertility treatments

Two standard fertility treatments were employed in field Experiment 2, which involved addition of N:P:K compound agricultural fertiliser at an application rate of 100 kg ha^{-1} plus a control. The standard field application rate of 100 kg ha^{-1} was derived by comparing the agricultural (e.g. Soffe, 1995) and forestry literature (e.g. Lambert *et al.*, 1994; Munson *et al.*, 1995) on fertilisation for fodder and timber production, respectively, and after taking agronomic and forestry advice. As with the light treatments, ease of replication and measurable divergence of ground flora response were the main objectives. All fertiliser was applied by hand in 50 kg ha^{-1} doses, three weeks apart, to minimise scorching of vegetation and osmotic shock to seeds. Experiment 3 with the artificial ground flora communities provided an opportunity to further experiment with fertilisation rates. In this experiment three fertility treatments (N:P:K compound agricultural fertiliser at 100 and 200 kg ha^{-1}, plus a control) were employed to replicate fertilisation in the field (Experiment 2) and to provide double the standard field application rate.

2.2 Sites

2.2.1 Wolverhampton Environment Centre

The Wolverhampton Environment Centre is located in Finchfield, Wolverhampton (O.S. Grid Ref. SO 879982) and now forms part of the Smestow Valley Local Nature Reserve. The site was previously the Council's Central Plant Nursery, which was abandoned for this purpose *c.* 10 years ago, and since then the tree nursery trees have grown to form well defined, dense, largely monospecific plantations of *c.* 15 years in age. These uniform plantations provided ideal opportunities for replicated plot experiments. The relatively artificial and infertile substrate provided an analogue for urban soils. Soil compaction coupled with a perched water table dispose parts of the site to winter flooding. The light manipulation field Experiment 1 was established at The Wolverhampton Environment Centre.

2.2.2 Nedge Hill

This is a *c.* 30 year old mixed plantation on former agricultural land, which was landscaped prior to planting (O.S. Grid Ref. SJ 718069). Soils are relatively sandy and free draining and form part of the Bromsgrove Series (Ragg *et al.* 1984). The site is crossed by approximately 10 m wide grassy rides. Tree species are mainly native broadleaves, such as *Fraxinus excelsior* and *Quercus robur*, but exotics like ornamental cherry (*Prunus* spp.) are frequent, as are conifers, mostly *Larix decidua.* A row of larch

flank the ride next to the experimental area and form the edge of the 5 m wide buffer zone which screens the north eastern boundary of Experiment 2 from ride side light. A shrub layer of *Crataegus monogyna* and suckering cherry is fairly dense in places. The site occupies a semi-rural location, but usage is urban amenity due to its close proximity to Telford. Cohn (1994) successfully enhanced ground flora communities in experiments on this site. The soil fertility and light manipulation field Experiment 2 was established at Nedge Hill.

2.2.3 Plant and Environment Research Unit

The University Plant and Environment Research Unit at Compton Park, Wolverhampton (O.S. Grid Ref. SO 889989), formerly known as the Crop Technology Unit, is an area of gently sloping north facing land with relatively free draining sandy loams of the Saltwick series (Ragg *et al.*, 1984). Much of the site is under agricultural cultivation with managed grassland in between. Topsoil for use in Experiment 3 was collected from an area of abandoned arable land known as the 'barley field'. The polytunnel (a polythene shade tunnel with open mesh sides), used in Experiment 3, is situated on fairly even ground at the Plant and Environment Research Unit. The polytunnel has an E-W orientation and an internal light climate of approximately 30% ambient PAR. The soil fertility and light manipulation polytunnel Experiment 3 was established at The Plant and Environment Research Unit.

2.2.4 The Ercall and Wenlock Edge

The Ercall, near Telford, (O.S. Grid Ref. SJ 647098) is an ancient semi-natural mixed deciduous woodland covering an area of complex geology (Cambrian siltstones and shales overlain with boulder clay (Burnham and Mackney, 1964). The area used in the current research for seed and topsoil acquisition (Experiment 3) was on calcareous boulder clay with vegetation characteristic of the W8 - *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland community (Rodwell, 1991).

Wenlock Edge in Shropshire (O.S. Grid Ref. SO 604999) supports ancient semi-natural woodland on Silurian limestone. A limited amount of seed was also collected from East Wall Coppice, Wenlock Edge (O.S. Grid Ref. SO 538926) and Benthall Edge, Ironbridge (O.S. Grid Ref. SJ 667033). All plant communities used for seed collection can be described as calcareous ancient semi-natural mixed deciduous woodland (W8) and are situated within a 30 mile radius of Wolverhampton.

2.3 Seed mix

A standard native woodland ground flora seed mix, based on previous experimental work (Cohn, 1994), and designed to be representative of target (W8) ancient semi-natural woodland ground flora communities (Rodwell, 1991), was uniformly sown across all experimental plots. Most of the seed was bought; the few species unavailable commercially were collected locally from ancient semi-natural woodland sites described in Section 2.2.4. In all cases current year's seed and local provenance were guaranteed as far as practicable. All seed was dry and dark stored at 5°C prior to sowing.

Seed was bulked in silver sand immediately before sowing, to aid even application. The standard application rate of 100 seeds m^{-2} was employed where availability allowed, with the exception of the grasses where plant and seed size dictated a reduced rate of approximately 30 seeds m^{-2}. Table 2.1 illustrates species, sources, collection dates, application rates and sowing dates employed in the various experiments.

2.3.1 Germination trials

Germination trials, using the methods of Grime *et al.* (1981), were undertaken employing two cold storage treatments: damp sand in the greenhouse and peat-based potting compost subjected to a natural vernalisation prior to being placed under greenhouse conditions. Greenhouse conditions consisted of natural light and 25° / 15°C day and night temperatures. The number of seeds germinating in each treatment was recorded (seedlings were removed upon counting to avoid confusion) until there had been no germination for four weeks. These trials were undertaken to ensure a reasonable threshold of seed viability and to test for dormancy, of both bought and collected seed, prior to experimental establishment. Detailed results are not presented in the thesis; however, reasonable germination thresholds for most species were obtained following natural vernalisation, which was provided by autumn sowing in the experimental programme.

2.4 Light monitoring

Light monitoring was carried out in Field Experiments 1 and 2 during the woodland dark and light phases of summer 1999 and winter 1999 / 2000, respectively. In Experiment 3 light monitoring was carried out at regular intervals during the 1999 / 2000 growing seasons. Survey dates for light monitoring for the three experiments are given in

Sections 3.2.2, 4.2.2 and 5.2.2. All light monitoring was carried out during periods of evenly overcast weather, with low wind speeds, to minimise fluctuation in readings.

Photosynthetically active radiation (PAR) was measured simultaneously inside and outside the plantations / polytunnel, using two light meters. The light meter used to measure PAR inside the plantations / polytunnel was a Macam Q102 Radiometer with a PAR Sensor, set to measure PAR (μmol m^{-2} s^{-1}). The light meter used to measure ambient PAR outside of the plantations / polytunnel consisted of a PAR Quantum Sensor (QS-278) connected to a Fluke 79 III True RMS Multimeter. The resulting output in mV was multiplied by the conversion factor 1000/10.08 to obtain PAR (μmol m^{-2} s^{-1}). The two light meters had previously been calibrated against each other in the growth chamber at the Plant and Environment Research Unit.

The PAR measurements within the plantations / polytunnel were taken centrally within quadrats; those outside of the plantations / polytunnel were taken at the nearest fixed point experiencing full sunlight. The simultaneous PAR readings were recorded at a constant height above the ground, at 1.12 m in field Experiments 1 and 2 and at 0.4 m in Experiment 3. These constant monitoring heights were designed to coincide with the top of the field layer canopy in field Experiments 1 and 2 (e.g. Reader and Bricker, 1994), and with the average height of the vegetation, inside the shade tents, in Experiment 3. Mean sample PAR measurements were expressed as a percentage of the average ambient solar radiation reaching open ground adjacent to the plantation / polytunnel. A Quantum stopwatch was used to record the timing of the light readings. The ambient light intensity within the polytunnel was recorded on each occasion for comparison. As PAR measurements were not taken during the first year in Field Experiments 1 and 2, the percentage tree canopy cover above each quadrat was recorded at the time of the vegetation survey to provide an inverse analogue for light climate. The internal environment of the polytunnel (Experiment 3) was continuously monitored using a thermohygrograph to measure air temperature and relative humidity, for the duration of the experiment.

2.5 Vegetation survey

All ground flora vegetation within field experiments was surveyed during spring / summer of 1998 and 1999 using the following methodology. In field Experiments 1 and 2, 2 m × 2 m quadrats were employed as a sampling unit, as most appropriate for the

scale and heterogeneous nature of woodland ground flora vegetation. Quadrats were placed uniformly across experiments and centrally within treatment plots (or divisions thereof) to maximise sample area, while avoiding seeding plot buffer zones in order to minimise sowing plot edge effects. The sampling strategies for the field experiments are given in Sections 3.2.3 and 4.2.3. In Experiment 3, with the artificial ground flora communities, each box was treated as a sampling unit (Section 5.2.3). Precise survey dates are given in Sections 3.2.3, 4.2.3 and 5.2.3.

Within each quadrat the percentage cover and Domin values of all species of vascular plant were recorded. Species considered to form part of the canopy or shrub layer were not recorded (except in Experiment 2, see below). Bryophytes were recorded collectively as % cover. Percentage cover of bare ground, litter, woody brash and canopy cover were also noted. Woody brash was defined as woody debris with > 5 cm average diameter; anything smaller was recorded as litter. Densities of the introduced species (i.e. the number of individual plants) were recorded within each quadrat.

A phenological diary was kept, for all three experiments, throughout both growing seasons where general observations, particularly those relating to the introduced species were recorded. The baseline (pre-establishment) vegetation within experimental plots was also recorded in this way. The physiognomy of the vegetation response, in all experiments, during both seasons, was recorded photographically. In Experiment 2, at Nedge Hill, the percentage cover and density of species in the canopy and shrub layers were recorded within each treatment plot, to describe the complex nature of the tree canopy.

The artificial communities of Experiment 3 were recorded more frequently and a greater number of vegetation parameters were measured than in the longer term field Experiments, 1 and 2. The vegetation was surveyed on five occasions. Table 5.1 shows the survey dates and the parameters recorded at each survey, which are explained in Section 5.2.3.

2.6 Soil survey and analyses

The objective of the soil survey was to measure soil fertility across the experiments. The aim was to estimate spatial baseline (pre-establishment) fertility data and to detect any treatment influences. In order to achieve this the three major soil macronutrients were

measured in a form available to plants (mineralisable nitrogen, extractable phosphorus and potassium). Soil pH and organic matter content were also measured because of their likely influence on soil fertility (e.g. McCrea, 1999). The 'snap-shot' soil sampling strategy employed in the current research was considered too minimal to pick up meaningful results with respect to soil moisture. While the potential importance of mycorrhizal associations is acknowledged (Section 1.7.4), the quantification of their influence on community response is beyond the scope of this study.

2.6.1 Sampling and soil preparation

The soil sampling programme was undertaken to coincide with predicted maximum growth of field layer plants and hence probable maximum nutrient uptake. Sampling was carried out on 27/05/99 in the two field Experiments, 1 and 2, and immediately after the biomass harvest (11/5/00–22/5/00) in the experimental ground flora communities of Experiment 3. Topsoil samples were collected, using a trowel, at a depth of 5-15 cm (any litter or turf was not counted as part of this depth). The soil sampling strategies for each experiment are described in Sections 3.2.4, 4.2.4 and 5.2.4. In the field experiments a common approach was taken to produce a single soil sample for each treatment replicate, consisting of at least five bulked individual soil samples. The aim was to gain a broad indication of the pattern of soil fertility across the experimental areas and to detect any treatment effects. In Experiment 2 further detailed sampling was undertaken (bulking five soil samples from each quadrat) within the first light treatment replicate to provide a more detailed insight into within plot variation. In Experiment 3, five soil samples were bulked to produce a sample for each quadrat or soil box.

Soil samples were air-dried at 40°C. The soil fine-earth fraction was then separated by sieving the dry soil with a 2 mm mesh sieve. The dry fine-earth fraction, which was used for all subsequent chemical analyses, was thoroughly mixed before being stored in airtight plastic bags. Prior to each analysis, samples were re-mixed and sub-sampled to produce two replicates per sample for each chemical analysis. Extractable phosphorus and potassium, mineralisable nitrogen, plus soil pH and percentage organic matter were measured, as described below.

2.6.2 Soil pH

10 g samples of sieved (< 2 mm) air-dried soil were mixed with 25 ml of distilled water for five seconds and allowed to settle for approximately ten minutes. The samples were then re-mixed for a further five seconds and the pH of the solution was measured using a calibrated Hannah pH meter, once the reading had stabilised (Avery and Bascomb, 1982).

2.6.3 Mineralisable nitrogen

Two 5 g sub-samples of sieved (< 2 mm) air-dried soil were used to compare the ammonium content of the soil in its current state and after mineralisation (ammonification) caused by incubation. One sub-sample was placed in a glass test tube with 16 ml of distilled water. The tube was sealed with porous polythene film and incubated at 30°C for 14 days. The soil water solution was then steam-distilled with 16 ml of 4M KCL and 0.2 g of MgO. Then 10 ml of 2% boric acid indicator solution was added to the distillate after two minutes. The ammonium content of the solution was determined by titration with HCl. The distillation process was carried out immediately on the non-incubated sub-sample. The mineralisable nitrogen (mg kg^{-1}) was calculated by subtracting the ammonium content of the non-incubated soil from that of the incubated sub-sample (Dolmat *et al.*, 1980; Allen *et al.*, 1989; Page *et al.*, 1982).

2.6.4 Extractable phosphorus

The Olsen extraction method was employed. 0.5M sodium bicarbonate solution was added to 5 g sieved (< 2 mm) air-dried soil samples. The pH of the solution was adjusted to 8.5 using NaOH solution. Samples were then mixed on a rotary shaker for 30 minutes at 175 mot/min. The resulting soil solution was filtered through Whatman No. 91 filter papers and the filtrate collected. Phosphorus concentrations were determined by the blue phosphomolybdate spectrophotometric determination method. A standard ammonium molybdate solution was prepared by mixing 12 g of ammonium molybdate powder and 0.3 g of antimony potassium tartrate (to act as a catalyst) with water and 148 ml of concentrated sulphuric acid to make a 1 litre stock solution. This solution was diluted eight times in distilled water to make up the standard ammonium molybdate solution. For each sample a 10 ml aliquot of soil filtrate was mixed with 1 ml 1.5M sulphuric acid (to release the CO_2). Water was then added followed by 8 ml of ammonium molybdate solution and 8 ml of ascorbic acid solution. The extract was then made up to 100 ml with distilled water and left to stand for 20 minutes to allow the blue phosphomolybdate colour to develop. The UV absorbance of the phosphomolybdate blue colour was

measured at 880 nm using a Perkin-Elmer spectrophotometer (Allen *et al.*, 1989). The phosphorus concentrations (mg kg^{-1}) in each sample were determined by reference to a standard calibration curve created from potassium dihydrogen orthophosphate standards which were treated in the same way as the soil filtrates (Rowell, 1994).

2.6.5 Extractable potassium

Potassium was extracted from each 5 g sample of sieved (< 2 mm) air-dried soil using 50 ml of 1M ammonium acetate. Samples were then mixed on a rotary shaker for an hour at 175 mot/min. The resulting soil suspension was filtered through Whatman No. 91 filter papers and rinsed through with successive 25 ml aliquots of ammonium acetate, until 100 ml of filtrate had been collected. The potassium concentrations (mg kg^{-1}) in each sample were measured using a Corning 400 flame photometer and by reference to a standard calibration curve created from potassium solution standards (made by diluting potassium nitrate in ammonium acetate) (Rowell, 1994).

2.6.6 Soil organic matter

The loss-on-ignition method was used to determine the percentage of soil organic matter (Rowell, 1994). 20 g samples of sieved (< 2 mm) oven-dried soil were weighed into pre-weighed crucibles and heated at 375°C for 16 hours in a muffle furnace (Ball, 1964). Samples were then cooled in a desiccator and re-weighed. The loss of weight was recorded as a percentage of the initial oven-dry weight.

2.7 Statistical analyses and data presentation

2.7.1 Environmental variables

2.7.1.1 Surfer mapping

Key environmental variables in field Experiments 1 and 2 (including those identified as a significant influence on the vegetation by the Monte Carlo Permutation test in CANOCO 4 (ter Braak and Smilauer, 1998) (Section 2.7.2.2)) were spatially mapped using kriging as a method of data interpolation, performed in the Surfer software package. Surfer 6.01 (Golden Software Inc., 1993-1995), a contouring and 3D surface mapping system software, was used to generate contour maps. The key environmental variables included those relating to surface microclimate, such as bryophyte and litter cover, as well as variables relating to the light climate and soil environment. The contour maps produced give only a graphical representation of the distribution of environmental variables, due to the nature of the software and minimal datapoint coverage. Environmental variable

mapping was carried out to aid interpretation of CANOCO analyses (Section 2.7.2.2) and hence clarify significant environmental influences on the vegetation. In Experiment 2 the response variable, density of introduced species, was mapped in the same way to aid interpretation of CANOCO analyses. Contour mapping of key environmental variables was not carried out in Experiment 3, as both the light and soil environment had been manipulated in discrete units and not across continuous habitat.

2.7.1.2 Parametric analyses

The statistical distributions of all environmental data (including density response variables) were tested for normality using skewness and kurtosis measures. Although most ecological data are not normally distributed and most of the statistical methods employed do not require full normality, the results are more meaningful if data are as near to normal as possible (Legendre and Legendre, 1998). The data were transformed when the skewness and / or kurtosis value was > 1 (giving transformation of skewed data higher priority) and when a transformation which improved the normality of the data was available. Most of the environmental variables were measured on analytical scales, unrelated to ecological processes, which therefore are as appropriate for use in statistical analyses as the transformed data (Legendre and Legendre, 1998). The species data recorded on the Domin scale, which approximates to a log scale, was used in statistical analyses, as they did not require further transformation. This normality testing and transformation was carried out on all environmental data prior to further statistical analyses, including Student's t-test, ANOVA and CANOCO analyses (Section 2.7.2.2).

In Experiment 1 between-treatment (within each plantation) and between-plantation environmental differences (relating to the light climate and soil environment) were investigated using the Student's t-test (performed using Microsoft Excel 97 software). The 'vegetation environmental variables' percentage cover of bryophytes, bare ground, litter and woody brash, plus species density response variables (Section 2.7.3.2), were also analysed in this way. Treatment-significant and plantation-significant results are presented in tables of treatment and plantation means, respectively. Standard errors, t-values and t-critical values (for both one- and two-tailed tests), significance levels and degrees of freedom are given in these tables. Where transformed data were used back-transformed means have been presented to show consistency with the t-test results. The presentation of results from t-test analyses on the vegetation response variables (i.e. the

introduced species density data, representing both total and that of individual species) are described in Section 2.7.3.2.

The more complex experimental designs of Experiments 2 and 3 necessitated the use of ANOVA to investigate environmental variation between treatments and blocks. The Genstat 5 Committee (1993) statistical package was used to perform ANOVA on all environmental variables (relating to both the light climate, soil environment and surface topography / microclimate, plus vegetation response variables (Section 2.7.3)) measured in both growing seasons. Details and rationale for the design of the ANOVA used in Experiments 2 and 3 are given in Sections 4.2.5.1.2 and 5.2.5.1, respectively, but both conform to a factorial design set up as a two-way ANOVA (in randomised blocks). All ANOVA were accompanied by the least significant difference *post-hoc* test.

Treatment-significant and block-significant results are presented in ANOVA tables and tables of treatment and block means, respectively. The mean square of each significant environmental variable for each source of variation (i.e. block, light treatment, fertility treatment and light treatment x fertility treatment) with significance levels and degrees of freedom are given in the ANOVA tables. In tables of means the effective standard error is quoted to maintain consistency with the ANOVA tables. Where transformed data were used, back-transformed means have been presented to show consistency with the ANOVA tables. Significant interactions between the light and fertility treatments (where both main effects are also significant) are presented as line graphs. The presentation of results from ANOVA on the vegetation response variables, the biomass, height, recruitment and density data are described in Section 2.7.3.

2.7.2 Vegetation and environmental data: Multivariate analyses

The multivariate vegetation data collected in Experiments 1, 2 and 3 were analysed by classification and ordination techniques. These techniques elucidate the structure of the data, plus any relationships within it. Samples (quadrats) may be classified or ordinated according to their species composition; likewise species can be classified or ordinated according to their occurrence within samples. Although both sample and species classification and ordination were carried out, the analysis focuses on sample classification and ordination as providing most information on plant community composition. These multivariate analyses are used to describe plant communities and to investigate the influence of environmental factors on these communities.

2.7.2.1 Classification: TWINSPAN analyses

The TWINSPAN (TWo-way INdicator SPecies ANalysis) (Hill, 1979a) routine of the VESPAN III software package (Malloch, 1999) was used to produce classifications of both sample and species data, from both seasons in field Experiments 1 and 2. This was done to aid description of the plant communities which developed following species introductions. The discrete box-communities of Experiment 3 were not considered suited to this type of analysis. TWINSPAN combines ordination and clustering, using a hierarchical polythetic divisive algorithm to classify multivariate data. TWINSPAN is a robust effective classification technique (also known as dichotomised ordination analysis) which is extensively used in plant ecology (e.g. Gauch, 1982; Kershaw and Looney, 1985; Kent and Coker, 1995). However, TWINSPAN may be limited as an aid to plant community description in studies where the vegetation or primary data set has a short gradient length under Detrended Correspondence Analysis (DCA) (Vaz, 2001). TWINSPAN is based on DCA, which is a unimodal model; linear models, such as PCA, provide a closer description of data variation in small data sets (ter Braak and Smilauer, 1998; Legendre and Legendre, 1998) (Section 2.7.2.2).

Samples are ordinated by reciprocal averaging and then divided into two groups at the mean of the sample scores. TWINSPAN then identifies 'indicator' or 'differential' species that are preferential to either sample group; these species are used to refine the ordination, which is divided as before. The analyses are then repeated and all sample groups are further subdivided until a pre-determined minimum group size is reached (Maddy and Brew, 1995). In the current research a group size of five samples was used as a pre-set minimum. TWINSPAN uses 'pseudospecies' which shows the abundance of either 'indicator' or 'differential' species allowing a more detailed ecological interpretation of the classification. Each species is represented by up to four 'pseudospecies' (or abundance) levels that are determined by their Domin value. The 'pseudospecies' levels are 1, 2, 3 and 4, representing low to high abundance, respectively. The 'pseudospecies' levels are cumulative, so that level 2 incorporates level 1, and so on. The classification of the species (which is produced after the sample classification) allows TWINSPAN to construct an ordered two-way final table that visually displays both the classification and ordination of the samples and species simultaneously.

The information generated by the TWINSPAN sample classifications has been displayed in dendrograms (Legendre and Legendre, 1998), to aid ecological interpretation. Groups to which a defensible ecological interpretation can be given and which are not so small in terms of stand / species numbers that they could be considered to have arisen by chance are shown, and are referred to as 'end groups'. Further divisions beyond end groups are not considered. Because TWINSPAN places samples with similar floristic composition together in groups, these end groups approximate to plant communities. Binary notation is used to label the sample groups on the dendrogram and the number of samples within each group is given. At each division on the dendrogram indicator species are shown, in order of importance, with pseudospecies levels in brackets. Indicator species are those species identified by the program as being particularly diagnostic for each division. Where no indicator species are given, preferential species with pseudospecies levels are shown (preferential species are shown inside square brackets in the figures). Preferential species are similar to indicator species, i.e. they are still associated with either the negative (left-hand) or positive (right-hand) side of a division, but are less diagnostic of divisions. The most important preferential species are also included when indicator species are too few for effective interpretation. In dendrograms in Experiment 1, the percentage of samples from each light treatment is given at each TWINPSPAN division, to aid interpretation of treatment effects on the vegetation. TWINSPAN end group maps were also produced to show the distribution of the main vegetation 'communities' within the field experiments.

2.7.2.2 Ordination: CANOCO analyses

Ordination techniques arrange samples and species along axes of variation, in a way that places similar samples or species close together and dissimilar ones further apart. Ordination is particularly useful in describing the continuous variation found in plant communities. Ordination techniques perform linear transformations of the multivariate vegetation data, by rotation, to extract axes of variation that account for variation within the data set. The first axis of variation will explain the largest proportion of the variance within the data; the second axis (perpendicular to the first) explains the next largest proportion of the variance, and so on. Each axis of variation is given an eigenvalue, which indicates the proportion of the total variation in the data that it describes. Eigenvectors show the relationship between each variable and the axes in multi-dimensional space. Ordination techniques can be unconstrained (indirect gradient analysis), in which samples are arranged according to their floristic composition only and

any environmental interpretation of the axes of variation within the data is independent of the analyses. Alternatively, ordination techniques can be constrained (direct gradient analysis). In direct gradient analysis the ordination of the vegetation data is constrained by a second data set representing the environmental variables. Direct gradient analysis aids ecological interpretation of environmental influences on the vegetation and allows statistical testing of the significance of each environmental variable using Monte Carlo permutation tests (ter Braak and Smilauer, 1998).

Within ordination techniques two types of model are used, depending on the scale of variation within the primary or response data set (i.e. the vegetation data): linear and unimodal models. The linear model approximates a simple linear response along an environmental gradient and is usually fitted by the least squares regression method (Leps and Smilauer, 1999). For primary data sets with a short gradient length, the response of this data set to the environmental data set is assumed to be linear. However, primary data sets with longer gradients (i.e. greater variation) require a non-linear unimodal response model, where each species exhibits an optimum on the environmental gradient. A weighted-average is used to estimate the unimodal response. For each environmental variable the optimum of the species response is the average of the values of the variables within the samples in which the species occurred, weighted by the relative species abundance (ter Braak and Smilauer, 1998). Linear response models include Principal Components Analysis (PCA) for unconstrained ordination and Redundancy Analysis (RDA) for constrained ordination. Unimodal response models include Correspondence Analysis (CA) and Detrended Correspondence Analysis (DCA) for unconstrained ordination and Canonical Correspondence Analysis (CCA) for constrained ordination (Leps and Smilauer, 1999). All of these techniques are widely used in plant ecology (Gauch, 1982; Randerson, 1993). All multivariate analyses were performed using CANOCO 4, a FORTRAN program for CANOnical Community Ordination (ter Braak and Smilauer, 1998).

Detrended Correspondence Analysis (DCA) (DECORANA (Hill, 1979b)) uses detrending by segments to overcome the two main disadvantages of Correspondence Analysis (CA), the arch effect and compression of data points at the ends of the axes, both of which may confuse ecological interpretation. In DCA the first axis of variation is divided into segments and the scores on the second axis are adjusted accordingly, so that the mean scores of all segments are equal (Hill and Gauch, 1980). The scores are then

distributed evenly along the first axis. Although detrending can aid ecological interpretation, it can obscure natural patterns within the data (Maddy and Brew, 1995). In the current research DCA is used to determine the gradient length of the primary data set and therefore the type of response model to be used. When detrending by segments the standard deviation (SD) of the species are used to scale the axis. The maximum gradient length in DCA approximates to the length of the ecological gradient. Data sets with short gradients (< 3 SD) are best investigated using linear models and those with longer gradients (> 4 SD) should be analysed using unimodal models (ter Braak and Smilauer, 1998; Legendre and Legendre, 1998). In all experiments the gradient length of the vegetation data was short (investigated by DCA), so only linear models PCA and RDA were used, and are described in more detail.

Principal Components Analysis (PCA) is an unconstrained ordination technique that uses a linear response model. The ordination is based on the covariance matrix for the vegetation data and the correlation matrix for the environmental data, which effectively standardises the environmental data (Maddy and Brew, 1995). Analysis of both primary and explanatory data sets can be carried out under PCA by indirect comparison, where environmental variables do not affect the ordination, but their regression vectors can be represented passively on a biplot (Legendre and Legendre, 1998). In the current research PCA is used to investigate the vegetation data set, with and without passive representation of all environmental variables on the species scatter plot. This aids interpretation of species-environment relations as all variables can be viewed relative to each other and the vegetation. As this provides no direct correlation between the primary and explanatory data sets, direct ordination (RDA) is used to investigate the environmental influence on the vegetation. The ordination scores produced by PCA for the first two axes of variation are plotted as scatter plots, where samples are represented by points and the variables (in this case the species) are represented by vectors, originating from the centre of the biplot. The direction of the vector shows where, in ordination space, the variable has most influence and the length of the vector is proportional to the magnitude of its influence. For clarity PCA vectors (i.e. the species) are represented as labeled points on the scatter plots.

Redundancy Analysis (RDA) is a constrained ordination technique that uses a linear response model (i.e. it is a constrained version of PCA, where axes are constrained as linear combinations of the environmental variables (Maddy and Brew, 1995)). RDA is a

form of multiple regression applied to multivariate data (Legendre and Legendre, 1998). RDA models simultaneously the linear relationship between the primary (vegetation) and explanatory (environmental) data sets. The constrained ordinations produced by RDA are shown on triplots, with samples and species represented by points (rather than vectors, for reasons of clarity) and environmental variables represented by vectors.

Monte Carlo permutation tests are used in constrained ordination to test the statistical significance of the relationship between the species and the environmental variables (ter Braak and Smilauer, 1998). There is no reference distribution with which to compare the data in order to produce the test statistic. Instead the reference distribution is simulated by repeatedly and randomly permutating the data. The null hypothesis (H_o) is that the species response is independent of the environmental variable. The permutations can be constrained to take into account experimental design or time series data.

Partial analysis is carried out when the influence of an environmental variable (or set of variables) is so great as to obscure the remaining variation. Investigation of this remaining variation is achieved by partialling out the effect of the overriding variable, by treating it as a covariable, before the constrained ordination is carried out (Leps and Smilauer, 1999). Partial analysis can be undertaken, for example, to remove known effects due to experimental design or a gradient such as slope, acting across the experimental area (i.e. to remove plot position effects). Partial analysis also allows estimation of the amount of variation in the primary data set that can be attributed to one or more of the explanatory variables.

When building a response model in CANOCO, variance partitioning (forward selection) is used to analyse one environmental variable at a time (the remainder are treated as covariables). Selection of environmental variables, to determine their partial effect, can be carried out under manual or automatic selection, which allows ranking of variables in order of the amount of variation explained. Under manual selection the significance of each variable selected can be tested using a Monte Carlo permutation test (ter Braak and Smilauer, 1998). At each step the selected variable becomes the only explanatory variable and the remainder are ranked by their marginal effect, or the amount of variance that would be explained if they were included in the model. If the selected variable is significant ($p < 0.05$), under the Monte Carlo permutation test, it can be added to the model. In the current research the 'reduced model' was used for the permutation tests, as

it is likely to reduce the occurrence of Type I errors in small data sets (ter Braak and Smilauer, 1998). 'Unrestricted permutations' were used as it was felt that the parametric analyses took account of experimental design, whereas CANOCO analyses were being used to aid description of continuous variation within vegetation data. Once included in the model, the variable is treated as a covariable for the continued testing of the remaining variables. The model is built up as successive significant variables are added, in order of the amount of variance explained, during the selection process. The significance of each variable will depend on the order in which variables are added to the model. Stepwise forward selection is a useful technique in determining a subset of environmental variables which are sufficient to represent most of the relationships between the vegetation and the environment (ter Braak and Smilauer, 1998).

CANOCO was used firstly to confirm the gradient length (i.e. the scale of variation) of the vegetation data under DCA, then to carry out unconstrained ordination of the data using PCA and finally to build a model where the ordination was constrained by those environmental variables which were significant under manual selection, as tested by Monte Carlo permutations. Whilst carrying out manual selection, preference was given to the continuous measured variables which represented the nominal / ordinal treatment variables. A further method of statistical investigation for identifying treatment effects on the vegetation, developed by Jones (1993), was deployed. This involved performing a Student's t-test (Experiment 1) or ANOVA (Experiments 2 and 3) on the sample ordination scores for the first two axes of variation produced by the PCA.

Environmental variables representing soil fertility and the light climate, plus 'vegetation environmental variables' (Section 2.7.1.2) were examined against vegetation response using CANOCO, to investigate potential environmental influences on the establishment of introduced species and on the direction of vegetation development. The environmental variables measured in both seasons were used, along with the treatment variables, in direct gradient analysis of vegetation data from both years. As soil variables and PAR measurements were only obtained in the second year of the field experiments, these variables were only used in direct gradient analyses of 1999 vegetation data. This similarly applies to the soil data and Survey 4 in Experiment 3 (Section 5.2.5.2). Additional position variables were added to the CANOCO analyses of data from Experiment 2 due to the hypothesised slope effect on vegetation. The spontaneous vegetation data set, in Experiment 2, was investigated separately, with the introduced

species included as environmental variables in RDA (Section 4.2.5.2.2). Combining explanatory variables in interaction and partial ordination, were both used in RDA, in Experiment 3 (Section 5.2.5.2).

Ordination diagrams were created in CanoDraw 3.1 and modified in CanoPost 1.0 (ter Braak and Smilauer, 1998). In all ordination diagrams (biplots and triplots) samples were coded (by colour and shape / size) to differentiate between experimental treatments. Vectors arising from the primary data set are represented as labelled points on the ordination diagrams for clarity reasons. Sample numbers are shown in ordination *diagrams for Experiments* 1 and 3, but not in Experiment 2, for reasons of clarity. Continuous environmental variables, plus ordinal treatment variables, are represented by vectors in the triplots; whereas nominal treatment variables are denoted by their centroid. Species are colour coded according to whether they are introduced or spontaneous. Only those species which occurred in five or more quadrats and which best fitted the statistical model (using the 'Rules of visibility - minimum fit' function in CanoDraw) are shown in the ordination diagrams. Species are denoted by Latin names (Stace, 1997) abbreviated to the first four letters of the genus and specific epithet. In Experiment 3 some non-introduced woodland species arose from the woodland soil used in the compost. To avoid confusion with the introduced woodland species, the specific epithet is replaced with 'background', which is abbreviated to 'back'.

2.7.3 Vegetation response variables: Parametric analyses

2.7.3.1 Biomass and height data

Biomass and height data were only collected in the artificial ground flora communities of Experiment 3 (Section 5.2.3). ANOVA analyses (Section 2.7.1.2) were carried out on these variables to investigate treatment differences in terms of plant production and stature and to identify and investigate any plot position effects. Significant results are presented in ANOVA tables (Section 2.7.1.2) and treatment means are presented in bar charts. The biomass data was also used to construct a species abundance table for the three light treatments (Section 5.2.5.3).

2.7.3.2 Species density and recruitment data

In field Experiments 1 and 2 only density data for the introduced species were recorded, whereas in the experimental ground flora communities of Experiment 3, the densities of the spontaneous species were also measured. In Experiment 3 recruitment levels of

introduced species were calculated between surveys. In Experiment 3 density and recruitment data were analysed using ANOVA (Section 2.7.1) by individual introduced species and for the introduced and spontaneous species groups. In Experiments 1 and 2 density data were analysed using the Student's t-test and ANOVA, respectively (Section 2.7.1.2) on the individual introduced species density data and on the total density of the introduced species, to investigate treatment and block effects. Results from Experiment 2 are shown in the ANOVA tables and tables of treatment and block means, with the individual species density data shown in bar charts. Significant results from Experiment 3 are shown in ANOVA tables, tables of treatment means and bar charts. In Experiment 1, the total introduced species density results are presented in the table of means, whereas, the treatment means of the individual species density data are shown in bar charts, with t-values, significance levels and degrees of freedom given in the text (Section 3.2.5.3).

Table 2.1 Summary Information on the Seed used in the Standard Seed Mix.

Species	Source	Collection Date	Sowing Rate (m^{-1}) (no. seeds m^{-1})	Sowing Date		
				Expt. 1	Expt. 2	Expt. 3
Brachypodium sylvaticum	Wenlock Edge	2/10/97 + 9/10/98	30	23/3/98	14/2/98 + 15/2/98	21/1/99
Bromopsis ramosa	Wenlock Edge	31/10/97 + 9/10/98	30	23/3/98	14/2/98 + 15/2/98	21/1/99
Campanula trachelium	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Circaea lutetiana	Wenlock Edge	2/10/97 + 9/10/98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Digitalis purpurea	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Galium odoratum	East Wall Coppice / Benthal Edge	2/10/97 + 1/11/97	2	–	14/2/98 + 15/2/98	–
Hyacinthoides non-scripta	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Milium effusum	The Ercall	13/10/97 + 7/10/98	30	23/3/98	14/2/98 + 15/2/98	21/1/99
Primula vulgaris	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Scrophularia nodosa	East Wall Coppice	31/10/97	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Silene dioica	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Stellaria holostea	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99
Viola riviniana	Seed merchant	1997 / 98	100	23/3/98	14/2/98 + 15/2/98	21/1/99

Chapter 3: Light Manipulation Experiments: Experiment 1: A Field Experiment at the Wolverhampton Environment Centre

3.1 Introduction

Experiment 1 was designed to be a relatively simple investigation into the influence exerted by the complex woodland light climate on field layer development in urban secondary woodlands with enhanced ground floras. The simple nature of the monospecific plantations, with even planting and age structure (see Section 2.2.1 for site description), coupled with a single silvicultural operation to manipulate the tree canopy and influence irradiance reaching the woodland floor, was utilised. Quantification of ground flora responses to light intensity were measured at both community and species levels. The tree species present allowed an investigation of canopy species influence on soil fertility as well as on the woodland light climate.

3.1.1 Aims and objectives

The central aims of Experiment 1: The Light Manipulation Experiment at the Wolverhampton Environment Centre were to:

- Test the hypothesis that light intensity is a major determinant of vegetation development in enhanced ground flora communities.
- Define ranges of light intensity which optimise vegetation development in the direction of target communities (Section 1.4.1).
- Determine which soil fertility properties influence the direction of development of ground flora communities.

The objective of Experiment 1 was to investigate field layer plant communities that develop following species introductions in established plantations, in relation to variations in light regime (manipulated by selective canopy thinning) and soil fertility (background variation).

3.2 Methods

3.2.1 Establishment

Two *c.* 15 year old, 420 m^2, monospecific plantations at the Wolverhampton Environment Centre (see Section 2.2.1 for site description) with a fairly dense but uniform canopy, were selectively thinned on 16/03/98 and 17/03/98. This provided two light treatments, 100% and 50 % of current canopy cover, each replicated three times. Tree species in the respective plantations were Norway maple (*Acer platanoides*) and Italian alder (*Alnus cordata*). The two plantations were situated next to each other on even ground. Both experimental areas measured 30 m x 14 m and were immediately surrounded by an unthinned buffer zone, of at least 2 m. Each treatment plot measured 10 m x 7 m. Figure 3.1 shows the relative location and experimental layout of treatment plots.

Both plantations were raked prior to sowing with the standard seed mix (see Table 2.1 for seed mix details and Section 2.3 for application methods) on 23/03/98. The late sowing date, caused by unavoidable delays in site access, necessitated an artificial chilling. Seeds were kept imbibed in damp sand in sealed plastic bags, which were placed in a 5° C refrigerator and packed in ice for three weeks to break dormancy and prevent premature germination prior to sowing. Plates 3.1 and 3.2 illustrate the experiment at establishment in the Norway maple and Italian alder plantations, respectively; differences between the treatment plots are evident. Background vegetation is described in Section 3.3.1 (Plates 3.1 and 3.2).

3.2.2 Light monitoring

Light monitoring was carried out during the woodland dark and light phases, of summer 1999 (on 19/08/99 in the Norway maple plantation and on 31/08/99 in the Italian alder plantation) and winter 1999 / 2000 (on 23/02/00 and 10/03/00 in both plantations), respectively. Photosynthetically active radiation (PAR) was measured simultaneously inside and outside the plantations, as described in Section 2.4. Mean sample PAR measurements were expressed as a percentage of the average ambient solar radiation reaching open ground adjacent to the respective plantations. The percentage tree canopy cover above each quadrat was recorded at the time of the vegetation survey.

3.2.3 Vegetation survey

The field layer vegetation was surveyed during the spring / summer of both 1998 and 1999, as described in Section 2.5 (i.e. between 25/08/98 and 2/09/98, and 11/06/99 and 25/06/99). The late survey dates during the first growing season reflect the late sowing and establishment of this experiment. Quadrats were positioned as shown in Figure 3.1.

3.2.4 Soil survey and analysis

On 27/05/99, soil sampling was undertaken, as described in Section 2.6.1. Five topsoil samples were taken, one from the centre of each quadrat and one from the centre of the treatment plot, and these were later bulked to form a single sample for each treatment replicate. Soil samples were prepared and stored as described in Section 2.6.1. Chemical analyses were carried out to quantify indicators of soil fertility. Soil pH and mineralisable nitrogen, extractable phosphorus and potassium, plus percentage soil organic matter were measured, as described in Sections 2.6.2-2.6.6, respectively.

3.2.5 Statistical analysis and data presentation

3.2.5.1 Environmental variables

3.2.5.1.1 Surfer mapping

Key environmental variables and vegetation parameters (which were significant under manual selection in CANOCO (Section 3.2.5.2.2)), were spatially mapped using kriging as a method of data interpolation, performed in the Surfer 6.01 (Golden Software Inc., 1993-1995) software package (Section 2.7.1.1).

3.2.5.1.2 Parametric analyses

Student's t-tests were performed on all environmental variables (and 'vegetation environmental variables', i.e. percentage cover of bare ground, bryophytes, litter and woody brash, plus vegetation response measures i.e. the density of introduced species, (Section 3.2.5.3)) measured in both growing seasons to investigate between-plantation variation and treatment effects. Significant results are presented in tables of treatment and plantation means with standard errors (Section 2.7.1.2). The individual species density data are dealt with in Section 3.2.5.3.

3.2.5.2 Vegetation and environmental data

3.2.5.2.1 Classification: TWINSPAN analyses

All analyses described in this and the following Section (3.2.5.2.2) were carried out on data from the two plantations and the two growing seasons. The multivariate vegetation sample data were classified using TWINSPAN (Hill, 1979a), to aid description of the plant communities which developed in the first year, and to identify niches and communities into which introduced species have the potential to become established. Analysis of second season vegetation data was used to highlight consolidation of niches by introduced species and to track the early development of these enhanced ground flora communities. Results are displayed in dendrograms. TWINSPAN end group maps show the distribution of the main vegetation 'communities' (Section 2.7.2.1).

3.2.5.2.2 Ordination: CANOCO analyses

Environmental variables representing soil fertility (Section 3.2.4) and the light climate (Section 3.2.2.), plus 'vegetation environmental variables' (Section 3.2.5.1.2), were examined against vegetation response using CANOCO as outlined in Section 2.7.2.2, to investigate potential environmental influences on the establishment of introduced species and on the direction of vegetation development. The environmental variables measured in both seasons, the thinning treatment variable, percentage canopy cover, percentage cover of bryophytes and percentage of bare ground and litter, were used in direct gradient analysis of vegetation data from both years. As soil variables and PAR measurements were only obtained in the second year of the experiment, these variables were only used in direct gradient analyses of 1999 vegetation data. PCA results are presented in scatter plots and RDA results are presented in triplots (Section 2.7.2.2).

3.2.5.3 Species density data

To investigate whether the thinning treatment influenced the densities of introduced species, Student's t-tests (Section 2.7.3.2) were performed on quadrat density data (i.e. number of individual plants) for all introduced species (Σx) and individual species from both growing seasons. The treatment means of the individual species density data are shown in bar charts, with t-values, significance levels and degrees of freedom reported in the text. The treatment / plantation significant means of all introduced species (Den Intro) are reported in tables of means (Section 3.3.4).

3.3 Results

3.3.1 Physiognomy

Background vegetation can be seen in the establishment photographs (Plates 3.1 and 3.2) for the Norway maple and Italian alder plantations, respectively. There were clear visual differences between the two species stands. The Norway maple ground flora was a sparse vegetation dominated by tree seedlings, including Norway maple, and bryophytes. In contrast, the Italian alder plantation supported a taller and much more vigorous ground flora consisting of aggressive woodland and ruderal species, including abundant *Geum urbanum* and *Rubus fruticosus* agg.

It is hypothesised that this marked difference in baseline vegetation between the plantations was due to the different characteristics of the canopy species. Norway maple casts a very dense shade throughout much of the growing season. The large, slow-rotting leaves produce a barrier to the establishment of many species. In comparison, the Italian alder plantation had a more open canopy when in leaf (although denser planting may have offset this difference to some extent) and a less persistent litter layer. Alder species are known to fix nitrogen via actinomycetes (*Frankia alni*) in root nodules. Possibly a higher level of soil fertility was maintained beneath the alders, which interacted with the more favourable summer light climate to produce a more vigorous ground flora.

The first season (1998) vegetation response is evident in the photographs (Plates 3.3 and 3.4) for the Norway maple and Italian alder plantations, respectively. In the Norway maple plantation (Plate 3.3) *Silene dioica* and *Scrophularia nodosa* form a prominent feature of the vegetation. Introduced species were less prominent under Italian alder (Plate 3.4). Treatment plot boundaries were evident in the ground flora vegetation, but were less marked in the Italian alder plantation.

Second year (1999) vegetation in the Norway maple plantation is shown in Plates 3.5 and 3.6. Plate 3.5 illustrates detail of a tall herb community produced under a thinned canopy. This plant community is characterised by introduced species; *Silene dioica* dominates with abundant *Scrophularia nodosa* and *Brachypodium sylvaticum*. Plate 3.6 shows the stark contrast in response between treatments. The barren plot in the foreground shows little enhancement from baseline conditions, compared with the tall herb community in the thinned plot behind.

Second season vegetation response in the Italian alder plantation is illustrated in Plates 3.7 and 3.8 taken in thinned and control plots, respectively. The tall herb community occurring in the thinned Italian alder plots (Plate 3.7) is characterised, but not dominated by, introduced species. *Silene dioica* and *Bromopsis ramosa* are locally abundant with frequent *Scrophularia nodosa* and *Brachypodium sylvaticum*. In contrast, the control plot response in Plate 3.8 shows a tall herb community characterised by aggressive woodland and ruderal species, such as *Rubus fruticosus, Geum urbanum* and willowherbs, with only the occasional occurrence of introduced species.

In summary, the plant communities in both plantations exhibited a clear visual response to canopy thinning. A taller denser community was produced in thinned plots. The vegetation appeared to show abrupt interfaces between treatments in both seasons following thinning; no such boundaries were visible in the canopy. This was most evident in the second year in the Norway maple plantation (Plate 3.6).

3.3.2 Environmental variables

3.3.2.1 Light climate

It was hypothesised in Section 3.3.1 that the marked difference in background vegetation between the Norway maple and Italian alder plantations was due to the different characteristics of the canopy species. A visual comparison of light climate between species stands is shown in Figures 3.2 and 3.3 for the woodland dark and light phases, respectively. Clearly, the light regime in the Norway maple plantation is, overall, darker in the summer and lighter in the winter, compared to that of the Italian alder plantation. Figures 3.2 and 3.3 show a spatial correlation between thinning treatment and higher light levels. The results of t-tests on the light climate variables (i.e. mean PAR reaching the woodland floor during the woodland dark (PARD) and light phases (PARL), percentage canopy cover recorded in the 1998 (Canopy 98) and 1999 (Canopy 99) woodland dark phases) are shown in the tables of means for treatment and plantation significant variables (Tables 3.1 and 3.2, respectively).

Treatment differences in light climate within plantations are evident in Figures 3.2 and 3.3 and in Table 3.1. Thinning treatment had a highly significant impact on the light regime during both woodland dark and light phases and in both plantations (Table 3.1). A higher light climate was evident in thinned plots regardless of which light climate variable was investigated. Contour maps illustrate the more marked difference in

summer light climate between treatments in the Italian alder plantation (Figures 3.2 and 3.3). The Norway maple plantation exhibited greatest temporal (between seasons) variation in light climate, whereas in the Italian alder plantation, spatial variation (between thinning treatments) in the summer light climate was greatest.

Differences in light climate between the two plantations were evident (Figures 3.2 and 3.3, Table 3.2). Dark phase plantation comparisons of PAR reaching the woodland floor (Table 3.2) show no statistical difference between second season summer light climates, although the Italian alder canopy was thinner in 1999 (Table 3.2). However, plantation light climate differed significantly during the winter, with higher average PAR levels in the Norway maple plantation than in the Italian alder plantation (Table 3.2). The lower winter light levels in the Italian alder plantation were due in part to physiognomy and in part to denser planting. The seasonal light climate in the Norway maple plantation varied over a greater range than that of Italian alder (Figures 3.2 and 3.3), which may have exerted a greater influence on the development of the ground flora vegetation. CANOCO analyses (Section 3.3.3.2) have been used to further identify which aspects of the woodland light climate have greatest influence on the vegetation.

3.3.2.2 Soil environment

It was hypothesised in Section 3.3.1 that a higher level of soil fertility was maintained beneath the alders, which, coupled with a more favourable summer light climate, produced a more vigorous ground flora. As outlined in Section 3.3.2.1, the summer light climate was not more favourable when canopy treatment is taken into account.

Figure 3.4 shows the spatial variation in mineralisable nitrogen across the two plantations. A nitrogen gradient is visible across both species stands, but is steeper in the elevated levels of the Italian alder stand. Soil mineralisable nitrogen was significantly higher under Italian alder than in the Norway maple plantation (Table 3.2). However, treatment differences were only found under Norway maple, where mineralisable nitrogen levels were higher in thinned plots (Table 3.1).

The spatial variation in extractable potassium is shown in Figure 3.5. Potassium concentrations were significantly higher in the Italian alder plantation than in the Norway maple plantation (Table 3.2). Treatment effects were neither clear nor significant (Table 3.1). Baseline conditions appeared more important than experimental treatment with

potassium and both species stands exhibited potassium gradients (Figure 3.5). The gradient in the Italian alder plantation correlates to some extent with the mineralisable nitrogen gradient, with levels increasing in a north-easterly direction. The lower and more uniform potassium concentrations in the Norway maple plantation are overlain by a 'hotspot', which relates to plot 4, one of the control plots. As this 'hotspot' is on the edge of the plantation near a ride, it is thought that it could represent an old burn site.

Figure 3.6 shows variation in extractable phosphorus concentrations across the two plantations. In contrast to nitrogen and potassium, phosphorus concentrations were much higher under Norway maple than under Italian alder (Table 3.2). The thinning treatment did not have a significant effect on extractable phosphorus in either plantation (Table 3.1). Phosphorus gradients correspond with those of nitrogen and potassium in the Italian alder plantation, and with the potassium 'hotspot' in the Norway maple plantation (Figure 3.6).

Figure 3.7 shows the spatial variation in pH across the two species stands. Soil in the Italian alder plantation was more basic than in the Norway maple plantation (Table 3.2). Thinning treatment did not affect soil pH in either plantation (Table 3.1). Background pH gradients occurred in both species stands with levels increasing in an easterly direction (Figure 3.7).

The percentage of soil organic matter was much greater in the Italian alder plantation than under Norway maple (Table 3.2). Soil organic matter was higher in thinned plots in both species stands (Table 3.1). However, organic matter was not a significant variable when analysed in CANOCO with the vegetation data (Section 3.3.3.3), so has therefore not been mapped.

In summary, the soil in the Italian alder plantation exhibited generally higher fertility levels (except for phosphorus) with higher pH and organic matter contents. A baseline fertility gradient existed across the plantation. The thinning treatment had no detectable effect on the soil environment within this plantation. In contrast, the Norway maple plantation had a less marked nitrogen gradient running perpendicular to that of the alder stand, and a potassium – phosphorus 'hotspot' in the central third of the plantation. Mineralisable nitrogen levels were significantly increased under a thinned canopy in the Norway maple plantation.

3.3.3 Vegetation and environmental data

3.3.3.1 Vegetation environmental variables

The woodland light climate and soil environment combine with other tree canopy characteristics (such as the depth and nature of leaf litter) and topography to produce a surface microclimate which influences field layer vegetation. This vegetation, in turn, influences the microclimate and germination niches, crucial to successful ground flora enhancement. The t-test results (Section 3.2.5.1.2) on the total density of the introduced species are presented in this section, as this variable is considered to represent a measure of vegetation response. The results for the individual species density data are considered to represent response at the species rather than community level, and are presented in Section 3.3.4.

It was originally hypothesised that the large, slow-rotting leaves of Norway maple produce a dense litter layer, which could act as a barrier to the establishment of many species. Litter covered a significantly greater area under Norway maple with correspondingly less bare ground (Table 3.2). Litter cover was greater in unthinned control plots in both plantations (Table 3.1), perhaps indicating the disturbance impact that thinning operations can have on surface microclimates and therefore vegetation. Litter cover has not been spatially mapped, as it was not found to be significantly correlated with the vegetation when analysed in CANOCO (Section 3.3.3.3). Despite the greater litter cover and comparative lack of bare ground in the Norway maple plantation, introduced species were more successful, in terms of numbers and coverage, in both years, under a Norway maple canopy (Table 3.2). Field observations indicated that bryophyte cover was positively associated with colonisation by introduced species. Bryophytes were far more abundant in the Norway maple plantation (Table 3.2), as evident in the bryophyte cover contour map (Figure 3.8). A treatment effect is apparent in the Norway maple plantation, with greater bryophyte cover occurring in control plots (Table 3.1). CANOCO analyses (Section 3.3.3.3) have been used to investigate the potential influence of bryophyte cover on the vegetation.

Mean percentage cover abundance of grouped introduced and spontaneous species in thinned and unthinned plots are shown in Figures 3.9 and 3.10 for the Norway maple and Italian alder plantations, respectively. In both plantations thinning was associated with greater abundances of both introduced and spontaneous species. In the first year spontaneous species occurred at greater abundances than introduced species in both

plantations. Introduced species abundance increased in the second year in both plantations. In the Norway maple plantation introduced species occurred at greater abundances than the spontaneous species in the second year (Figure 3.9).

3.3.3.2 Classification: TWINSPAN analyses

TWINSPAN classifications of samples (quadrats) from each of the two plantations and years are displayed in dendrograms (Section 2.7.2.1). To elucidate any differences between treatment plots, at each TWINPSPAN division, percentages of samples from thinned and unthinned treatment plots are shown, in bold type, assigned to the negative or positive group in the dendrograms (Figures 3.11-3.14). A sample classification performed on the entire 1998 data set for Experiment 1 clearly separates the Norway maple and Italian alder samples at the first division, indicating that the vegetation in each of these plantations is different, as described in Section 3.3.1. Further TWINSPAN analyses were carried out separately for the two respective plantations. It was considered that a separate analysis of each plantation (including CANOCO analyses described in Section 3.3.3.3) would best allow description of the vegetation and identification of significant environmental influences on the vegetation, without results being obscured by the relatively large differences between the two plantations. TWINSPAN end group mapping was conducted on the sample classifications of both plantations in 1999 (Figure 3.15).

3.3.3.2.1 Norway maple plantation

The dendrogram, Figure 3.11, shows the TWINSPAN classification of the 1998 vegetation data from the Norway maple stand. Group 0 is a homogeneous group, characterised by annual species indicative of disturbance and consists entirely of quadrats from thinned plots. By contrast, the larger Group 1 is more variable, but includes a greater proportion of perennial species, such as *Geum urbanum,* and consists mainly of quadrats from control plots.

The species composition of end Group 0, nevertheless, has much in common with the other Norway maple end groups (described below); i.e. a weedy woodland community with a high frequency of introduced species. However, there is a greater association of Group 0 with non-woodland and annual species, as well as with higher abundances of many introduced species. Thinning apparently created conditions, most notably significantly higher light levels (Section 3.3.2.1), suitable for colonisation by non-

woodland annuals, such as *Polygonum persicaria* as well as for the establishment of the introduced species.

Group 1 is further divided into a small group (Group 11) of samples with low stature non–woodland species, as indicators and preferentials, and Group 10, which is characterised by larger ruderal species and tree seedlings. End Group 11 also has high frequencies of spontaneous woodland species, such as *Geum urbanum* and *Epilobium montanum*, and introduced species are present in all samples. Group 11 occurs equally in thinned and control plots. This group exhibits a high mean bryophyte cover, which warrants further investigation (Section 3.3.3.3). Group 10 contains almost exclusively control plots and is associated with a higher mean percentage canopy cover (Table 3.1).

To summarise, in 1998, five months after establishment, the positive side of the Norway maple sample division represents a vigorous ruderal woodland community, occurring mostly in control plots. Introduced species are poorly represented in this vegetation. In contrast, the negative side of the Norway maple sample division, occurring exclusively under thinned plots, represents a weedy woodland community with fewer aggressive competitors (Grime *et al.* 1979) and more non-woodland annuals. Introduced species are well represented in this vegetation. Introduced species are preferentially associated with thinned plots under the Norway maple canopy.

The second season (1999) sample classification of the Norway maple vegetation data is shown in Figure 3.12. Figure 3.15 shows the relative location of 1999 samples, assigned to TWINSPAN end groups, and treatment plots on the ground. The most notable differences between the 1998 and 1999 sample classifications (Figures 3.11 and 3.12) are the increased occurrence of introduced species as indicators and the decrease in the treatment effect on the first division. The first division of the 1999 vegetation data has split a number of plantation edge samples, which comprise mostly samples from thinned plot 6, Group 1, from the rest of the samples. The thinned samples in Group 1 are highly influenced by edge effects (Figure 3.15, Section 3.3.3.2) and the community they represent consists of tree seedlings, non-woodland grasses and forbs. Introduced species are relatively scarce in this vegetation. In contrast, Group 0, which incorporates most samples from the most desirable vegetation of Group 0 in 1998, is represented by a high abundance of *Silene dioica* (4) and low abundance of *Hyacinthoides non-scripta* (1) and *Milium effusum* (1). *Silene dioica* consolidated its dominance of communities

represented by the negative half of the dendrogram in the second year, and *Hyacinthoides non-scripta* and *Milium effusum* were recorded for the first time.

The division of Group 0 produces two types of vegetation, Groups 00 and 01. The smaller Group 01 is characterised by non-woodland willowherbs and *Rubus fruticosus* agg. (2), with frequent non-woodland grasses and forbs, such as *Ranunculus repens*. This group is comprised exclusively of thinned samples, which were influenced by treatment plot edge effects (Figure 3.15). Introduced forbs are well represented in this community, especially *Silene dioica* at high levels of abundance and *Scrophularia nodosa* at moderate levels. The larger Group 00 comprises nearly all samples from control plots, plus three thinned samples, which due to position effect, share more similarities with control plots. The introduced woodland grasses *Milium effusum* (1) and *Bromopsis ramosa* (2) are associated with this community, along with Norway maple seedlings and low stature non-woodland annuals.

In the two year development of these enhanced ground flora communities in the Norway maple plantation, the introduced species expanded from their initial establishment in plots with a higher light environment, to become dominant over much of the experimental area (Figures 3.11, 3.12, 3.15, Plates 3.3, 3.5, Section 3.3.2.1). Thinning treatment effect on the vegetation appeared to have diminished in the second year, being associated with the second rather than the first TWINSPAN division (see CANOCO analyses in Section 3.3.3.3 for further investigation).

3.3.3.2.2 Italian alder plantation

The TWINSPAN analysis of the 1998 Italian alder samples is shown in Figure 3.13. Group 1 comprises nine samples characterised by a high abundance of *Geum urbanum* (3) and the preferential species *Galium aparine* (2). Group 1 occurs across light treatments and throughout the Italian alder plantation and is characterised by relatively high mean tree cover and low mean bryophyte cover, plus the lowest frequency of introduced species. Group 0 consists of 15 samples characterised by *Poa trivialis* (2) and introduced preferentials *Brachypodium sylvaticum* (2) and *Scrophularia nodosa* (1), plus the spontaneous species *Epilobium montanum* (1), a plant which is more closely associated with woodland habitats than the other *Epilobium* species present (Sinker *et al.* 1991).

Further differentiation of the vegetation at the division of Group 0 is mainly concerned with the greater abundance of *Poa trivialis* and tree seedlings in Group 00 and the greater abundance of *Geum urbanum,* bryophytes and introduced species in Group 01. Group 00 occurs more frequently under control plots and is associated with relatively high mean tree cover. Introduced species feature, but only the grasses occur in all samples. A relatively low mean bryophyte cover reflects the very high abundances of *Poa trivialis* and *Rubus fruticosus* agg., which physically cover or shade out much of the ground surface. Group 01 is almost confined to thinned plots which have a significantly higher light climate compared with unthinned control plots (Section 3.3.2.1). Comparison between end Groups 01 and 00 suggests that a combination of thinning and associated disturbance, plus the existence of an initially more open vegetation (suggested by the higher mean bryophyte cover), favour the establishment of introduced species. This could be due to the creation of germination niches and increased access to resources (light is far less likely to limit plant growth in thinned plots), as well as less competition for their acquisition.

To summarise the Italian alder sample classification, the positive side of the dendrogram represents a vigorous weedy woodland community in which introduced species are poorly represented (Figure 3.13). The larger negative side represents a slightly less aggressive community, where *Geum urbanum* is less dominant and the introduced ground flora is a more prominent feature of the vegetation. *Poa trivialis* is an indicator of high fertility levels (Sinker *et al.* 1991) and its greater significance in the Italian alder vegetation perhaps indicates higher soil fertility in this plantation (Section 3.3.2.2). Comparison of sample classifications for the two plantations suggests that the first division is more clearly influenced by light treatment in the Norway maple plantation and that the influence of thinning on the herb community in the Italian alder plantation is less clear. These findings are further investigated by CANOCO analyses in Section 3.3.3.3 (also refer to Section 3.3.2.1 on the light climate).

The second season (1999) sample classification of the Italian alder vegetation data is shown in Figure 3.14. Figure 3.15 shows the relative location of 1999 samples, assigned to TWINSPAN end groups, and treatment plots on the ground. There are very few differences between the first and second year sample classifications (Figures 3.13 and 3.14), except that Groups 00 and 01 are transposed. Sample distribution between end groups is almost identical. The spontaneous species which are indicative of the first

division, *Poa trivialis* and *Geum urbanum*, increased in abundance between the two recording years. This perhaps represents niche consolidation, as the communities develop with time. The negative half of the dendrogram, containing the more desirable communities, is preferentially associated with a greater number of introduced species in the second season.

3.3.3.3 Ordination: CANOCO analyses

The physiognomy (Section 3.3.1) and TWINSPAN analyses in Section 3.3.3.2 clearly demonstrate that the two tree plantations have different field layer communities. Within the plantations, however, the field layers were broadly uniform, with only quite subtle variations in composition. This within-stand data are more continuous in nature and therefore the ordination program CANOCO, which identifies trends or axes of variation within the vegetation, was utilised.

Table 3.3 shows the results of the Monte Carlo permutation tests performed during manual selection in RDA, which were used to select significant environmental variables for inclusion in the model. In all ordination diagrams, colour coding of samples is used to differentiate between thinning treatments. Sample numbers are also given, and can be located within the experiment by referring to Figure 3.1. Species are colour coded according to whether they are introduced or spontaneous. Nominal environmental variables are denoted by their centroid, whereas continuous variables are represented by vectors (Section 2.7.2.2).

3.3.3.3.1 Norway maple plantation

The scatter plot, Figure 3.16, illustrates the relative positions of both species and samples under a PCA analysis performed on 1998 vegetation data in the Norway maple plantation. T-test analyses of the sample ordination scores for the first two axes of variation show that light treatment had a significant effect on axis 1 scores (Table 3.1). No treatment effect was identified on ordination scores for the second axis of variation produced by the PCA.

The sample polarisation according to light treatment along axis 1, coupled with the statistical difference in sample scores between treatments, suggests that axis 1 represents the light climate. Most species, both introduced and spontaneous, were preferentially associated with a thinned tree canopy and hence a higher light regime. Interpretation of

the second PCA axis is less clear. Species distribution along axis 1 is fairly narrow, but a much wider spread is evident along axis 2. With the exception of *Viola riviniana*, the introduced species all lie within the top half of the biplot and seem to be associated with most of the spontaneous woodland species, such as *Hedera helix* and *Epilobium* species.

In contrast, the species in the lower half of Figure 3.16 represent a more grass-dominated community, with ruderal forbs and seedlings of some less shade-tolerant tree species, like *Quercus robur*. These species are almost exclusively associated with quadrats 22, 23 and 24 (see Figure 3.1 for sample location), which are anomalies within this experiment. Due to edge effects, which exposed these samples to the highest light conditions in the experiment (Figures 3.2 and 3.3), these samples have almost as much in common with the adjacent grassy ride as they do with the other woodland quadrats. Because of their position within the experiment, these quadrats were exposed to high levels of disturbance during thinning, which has, together with the higher light levels, influenced their floristic composition.

The RDA triplot of species, samples and environmental variables, Figure 3.17, shows the measured environmental parameters which were associated with the establishment of the vegetation in the Norway maple plantation. The significance of the thinning variable and its association with the first axis of variation supports the hypothesis that axis 1 represents light regime.

Bryophyte cover was the only other variable correlated with the establishment of the vegetation in the Norway maple plantation. Bryophytes were negatively correlated with thinning (Table 3.1). However, most introduced species were associated with thinned plots or relatively high bryophyte cover (Figure 3.17). The suppression of vascular plants under Norway maple led to increased bryophyte cover and increased colonisation by the introduced specialist shade-tolerant flora.

The PCA performed on the 1999 vegetation data in the Norway maple plantation is shown in the scatter plot, Figure 3.18. Thinning treatment had a significant effect on axis 1 ordination scores, whereas no treatment effect was observed for the second axis of variation (Table 3.1). As at establishment, the most important axis of variation in the 1999 vegetation data appears to be a light gradient. However, signs that treatment effect was beginning to diminish in the second season can be seen in Figure 3.18. For example,

sample distribution along axis 1 has a narrower amplitude and is less clear cut with respect to treatment received. It is worth noting that with regard to several features both axes in Figure 3.18 are transposed when compared to Figure 3.16.

In 1999, most introduced species were still associated with spontaneous woodland species and samples under a thinned canopy, or with those samples situated at the edge of control plots responding to the increased side light created by thinning. *Hyacinthoides non-scripta* and *Milium effusum* germinated in the second season and were associated with control plots and few other species. *Brachypodium sylvaticum,* a key community component, appeared in the second year to be spreading under higher light regimes than it was at establishment.

The RDA triplot, Figure 3.19, shows those environmental variables associated with the development of the vegetation in the Norway maple plantation in the second year. The first axis of variation broadly correlates with the two most significant variables, dark phase PAR and bryophyte cover. These environmental parameters are inversely related. The sample ordination indicates that light climate, as altered by the thinning treatment, still accounted for much explainable variation in the data. Although the nominal treatment variable, 'thinning', ceased to be significant in the second season, dark phase PAR incorporated the remaining treatment influence. Bryophyte cover was still an important factor in early community development.

The introduced species exhibited a wide spread along the light axis, with community constants *Silene dioica, Scrophularia nodosa* and *Brachypodium sylvaticum* competing well at higher summer light levels, though not in samples most influenced by edge effects (i.e. those occurring in plot 6). These introduced species were preferentially associated with thinned plots, relatively uninfluenced by edge effects, and few other species, indicating their dominance of these communities. At the opposite end of the light gradient, associated with control plots and a relatively high bryophyte cover, were the introductions *Campanula trachelium, Milium effusum* and *Hyacinthoides non-scripta.* Both *Milium effusum* and *Hyacinthoides non-scripta* were first recorded in the second season, when fewer germination niches remained in the thinned plots. Both species can tolerate high summer shade levels.

The second ordination axis was associated with a soil pH gradient that existed across the site (Section 3.3.2.2) and represents background variation, largely unaffected by experimental treatment. Introduced species were negatively associated with pH. Higher pH values were associated with a ruderal grassy woodland edge community, represented in samples from plot 6 (see Figure 3.1 for plot location) described above. Baseline environmental conditions, coupled with experimental edge effects, were compounded by thinning treatment in plot 6.

A comparison of the introduced species and associated species between the two growing seasons, suggests that where introductions were successful they came to largely dominate these communities with time. This is evidence of directional development towards desirable plant communities.

3.3.3.3.2 Italian alder plantation

The scatter plot, Figure 3.20, shows the PCA analysis performed on the 1998 vegetation data in the Italian alder plantation. T-test analyses of the sample ordination scores for the first two axes of variation show that thinning had no effect on axis 1 scores. Thinning treatment was significant in its influence on axis 2 scores (Table 3.1). The sample distribution along axis 2 broadly splits control and thinned plots. Anomalies in this distribution have been caused either by control plots responding to increased side light from thinned plots or an adjacent open ride, or by thinned plots being overshaded by canopy expansion of control plot trees into newly created gaps.

Most species, introduced and spontaneous, were preferentially associated with thinning. As in the Norway maple plantation, the introduced species were closely associated with spontaneous woodland species, such as *Rubus fruticosus* and *Epilobium* species. Introduced species are all grouped within the bottom left hand quadrant of Figure 3.20, with low scores on both axes of variation. These species have a narrow spread on the thinning axis (axis 2), but a wider spread on axis 1. Axis 1 is more difficult to interpret and seems to represent a continuum from desirable, albeit rather weedy woodland communities, towards a more vigorous ruderal community dominated by *Geum urbanum.* It is hypothesised that axis 1 represents a background fertility gradient, which exists across the plantation (Section 3.3.2.2). This hypothesis was tested under direct gradient analysis using RDA.

The RDA of the first season vegetation data in the Italian alder plantation is shown in the triplot, Figure 3.21. The thinning treatment variable was just significant under Monte Carlo permutations and was the only variable used to constrain the ordination in the RDA. Using a single nominal variable to constrain the ordination rather biases interpretation of the main axis of variation in the data. No other variables measured in the first season were significant in their influence on establishment vegetation. Greater insights may therefore be gained from analyses of second year data, when soil variables were measured and light levels (PAR) were measured directly with light meters.

Figure 3.22 shows the PCA results performed on the 1999 vegetation data. Both species and sample distributions appeared broadly similar to the 1998 results (Figure 3.20). Axis 2 still appears to represent a light gradient influenced by thinning treatment. Thinning treatment significantly influenced axis 2 ordination scores (Table 3.1). Axis 1 still represents a continuum from desirable weedy woodland communities, towards a more vigorous ruderal community dominated by *Geum urbanum.* As in the Norway maple plantation, *Milium effusum* became established in the second year and was associated with control plots and ruderals. As before, suitable germination niches in the thinned plots (least influenced by edge effects) would have been scarce by the second year of the experiment and *Milium effusum* is well adapted to the darker conditions of control plots.

The 1999 RDA, Figure 3.23, suggests that it is the nitrogen aspect of soil fertility that accounts for much of the variation explained by the first ordination axis. It had been hypothesised that thinning would increase mineralisable nitrogen in the second year, via greater light penetration leading to increased soil temperatures and microbial activity, coupled with the potential nitrogen source increase in the form of decaying tree stumps. However, baseline mineralisable nitrogen was not measured and thinning treatment had no significant relationship with nitrogen concentrations in the Italian alder plantation. Figure 3.4 shows the steep nitrogen gradient across the plantation. Evidence suggests that this gradient represents background variation and has been relatively uninfluenced by experimental treatment.

Most of the desirable introduced species and less aggressive spontaneous woodland species, such as *Epilobium montanum*, were negatively associated with mineralisable nitrogen. The more vigorous *Geum urbanum* and *Urtica dioica* were strongly positively associated with this fertility variable. Extractable potassium was also correlated with

early community development in the Italian alder plantation. This macronutrient was positively associated with competitive ruderal species like *Elymus repens* and *Galium aparine,* though its negative influence on introduced species was less marked than that of nitrogen. The third macronutrient, extractable phosphorus, influenced the vegetation to a lesser extent and appeared to be correlated with axis 2 and the light climate. The background fertility gradient across the Italian alder plantation (Section 3.3.2.2) is represented in both ordination axes and exerted greater influence on the vegetation than the light climate. This accords with Grime's (1979) theory that diversity is inversely proportional to fertility.

Evidence from the PCA and RDA of the 1999 Italian alder vegetation data clearly shows that axis 2 of the RDA triplot, Figure 3.23, correlates with the light climate, as influenced by thinning. However, the quantitative variable which best represents this light gradient is light phase PAR, or winter light climate. It is believed that the lower winter light levels in the Italian alder plantation (Section 3.3.2.1) may have been crucial for the development of a largely vernal woodland ground flora.

3.3.4 Species density data

Mean densities quadrat^{-1} of introduced species in 1998 in thinned and unthinned plots of the Norway maple plantation illustrate the relative success of establishment of the introduced species and the influence of thinning on this response (Figure 3.24). *Circaea lutetiana, Hyacinthoides non-scripta* and *Milium effusum* were not recorded in the first year. Most introduced species grew at higher densities in thinned plots, though only *Viola riviniana* ($t = 1.83$, $p < 0.05$, d.f. = 22), *Scrophularia nodosa* ($t = 2.54$, $p < 0.01$, d.f. = 22) and *Primula vulgaris* ($t = 2.57$, $p < 0.01$, d.f. = 22) occurred at significantly greater densities under a thinned canopy.

Figure 3.25 shows mean density data for the second growing season (1999) in the Norway maple plantation. The early development of the introduced vegetation mirrors that at establishment, in terms of relative species response. *Hyacinthoides non-scripta* and *Milium effusum* established in the second year. *Digitalis purpurea* declined to isolated plants in 1999, as treatment effects diminished. As in the first season, *Scrophularia nodosa* ($t = 3.38$, $p < 0.01$, d.f. = 22) and *Primula vulgaris* ($t = 1.96$, $p < 0.05$, d.f. = 22) occurred at significantly greater densities in thinned plots. In contrast, *Bromopsis ramosa, Campanula trachelium, Hyacinthoides non-scripta, Milium effusum*

and *Stellaria holostea* all grew at higher densities in control plots; although this difference was only significant for *Campanula trachelium* ($t = 1.89$, $p < 0.05$, d.f. = 22) and *Milium effusum* ($t = 2.57$, $p < 0.01$, d.f. = 22).

Figures 3.26 and 3.27 show the density response of introduced species in the Italian alder plantation in the two respective growing seasons. Establishment of the introduced species was less successful in the Italian alder plantation, although the density response followed a broadly similar pattern to that in the Norway maple plantation, in terms of species, relative magnitudes and thinning treatment effects. The failure of *Circaea lutetiana* to germinate and produce viable seedlings is common to both plantations, and is consistent with germination trials (Section 2.3.1). As under Norway maple, *Milium effusum* established in the second growing season in the Italian alder plantation, though only in control plots. This largely supports results obtained by Cohn (1994) which indicate that species which fail to establish in the first season are likely to be present in the second, although *Hyacinthoides non-scripta* failed to establish in both years in the Italian alder plantation (one plant was recorded in 1999). Again, *Digitalis purpurea* failed to persist into the second year.

The most notable exception to the similarity in response pattern between plantations in terms of species and relative magnitudes of the introduced species was the greater occurrence of *Silene dioica* in the Norway maple plantation. This can be explained by the preference of this species for semi-open habitats. It is hypothesised that the shade cast by the spontaneous tall herb canopy inhibited establishment of *Silene dioica* in the Italian alder plantation. *Scrophularia nodosa* ($t = 2.08$, $p < 0.05$, d.f. = 22), *Silene dioica* ($t = 1.88$, $p < 0.05$, d.f. = 22) and *Viola riviniana* ($t = 1.79$, $p < 0.05$, d.f. = 22) occurred at significantly higher densities in thinned plots in 1998, with only *Scrophularia nodosa* ($t = 1.97$, $p < 0.05$, d.f. = 22) still significant in 1999. In contrast to the Norway maple plantation, *Bromopsis ramosa* and *Campanula trachelium* apparently responded positively to canopy thinning.

Although the introduced species response in the Italian alder plantation followed a broadly similar pattern to that in the Norway maple plantation, actual densities were far lower for all species. The most likely explanation for this difference is the vigorous nature of the background vegetation in the Italian alder plantation, as shown by the TWINSPAN analyses in Section 3.3.3.2. The vigorous tall herb woodland vegetation of

the Italian alder plantation provided far fewer germination niches than the more open community of the Norway maple plantation. Subsequent seedling establishment was probably hindered by greater competition for light and soil resources in the Italian alder plantation. The higher soil fertility (Section 3.3.2.2) under the Italian alder cannot be readily exploited by introduced species if germination niches are rare and establishment severely restricted. A potential establishment barrier in the Norway maple plantation, the dense litter layer, was ameliorated by raking prior to sowing (Section 3.2.1), however, this is likely to have favoured the establishment of spontaneous, as well as introduced, species.

The significant influence of thinning treatment on the densities of certain introduced species during a single truncated growing season indicates the importance of the establishment environment. Establishment of introduced species was generally enhanced under a thinned canopy. Second season results represent the early development of ground flora communities, when some species were consolidating niches, e.g. *Scrophularia nodosa*, whilst others, such as *Digitalis purpurea,* were declining due to treatment effect diminishing with time, which was exacerbated by edge effects.

3.4 Discussion

The evidence highlighted clear differences between the two species plantations, in terms of the tree canopy affecting the most important environmental variables, light climate and soil fertility. The influence of canopy species on light climate and soil fertility affected baseline vegetation and the extent to which introduced species could infiltrate this vegetation.

Differences in canopy architecture were evident, e.g. the large shade casting leaves of the Norway maple produced a very dark summer light climate, which significantly influenced field layer plant distribution. The light regime under a Norway maple canopy appeared to span a greater range seasonally, while in the Italian alder plantation, spatial treatment differences during summer appeared more marked. Summer light climate was the most influential measured variable on the development of ground flora communities in the Norway maple plantation. However, it is the darker winter light climate under Italian alder which most correlated with field layer development. It might be expected that the largely vernal species introductions would be more influenced by winter or early spring light regime than by summer levels. Perhaps in the Norway maple plantation the

early spring light levels were not limiting, whereas, in the Italian alder plantation winter light climate may have been limiting for some species (Table 3.2). The winter light regime in thinned plots was comparable to that in control plots of the Norway maple plantation.

Bryophyte cover, in combination with the light climate, was associated with ground flora development in the Norway maple plantation. Bryophytes were negatively associated with PAR. Introduced species in control plots were able to take advantage of the enhanced microclimate in terms of moisture, nutrients and shelter, as light became limiting for non-woodland species. In the Italian alder plantation, bryophytes at much lower abundances, were associated with more open plant communities in thinned plots, which favoured establishment of introduced species. However, CANOCO analyses identified no significant relationship between bryophyte cover and vegetation in the alder plantation.

Although light alone may not have been limiting for introduced species, except perhaps during the summer in control plots of the Italian alder plantation, the combination of lower light levels and reduced niche availability, plus increased competition due to fertility enhanced background vegetation, perhaps helps to explain the less marked response of the introduced species in the Italian alder plantation. The influence on field layer development of both light and dark phase woodland light climates requires further investigation (Section 6.7).

Thinning treatment created a significantly higher light climate in both plantations and in both seasons, although the effect was less in the second year. Canopy treatment differences were exaggerated in the Italian alder plantation by the deaths of uncut trees in thinned plots. This was due to an original dense planting with no subsequent canopy thinning, which caused etiolated tree growth. These weakened trees, when no longer protected by surrounding specimens after thinning, simply snapped or blew down in the wind. This led to more marked canopy differences between thinning treatments than had been planned, affecting both light and dark phase light climates.

Thinning treatment significantly influenced the establishment and early development of enhanced ground flora communities, particularly by promoting the success of introduced species. Thinning also allowed spontaneous species to flourish. For example, in the

Norway maple plantation, non-woodland annuals were favoured by thinning. The disturbance created by thinning was probably a significant factor in the success of this plant group. These annuals are unlikely to provide any threat to the longer-term development of target ground flora communities, because as treatment effects diminish with time, the light climate will limit their persistence.

It was originally hypothesised that there would be higher soil fertility levels in the Italian alder plantation because of nitrogen fixing bacteria in root nodules. Soil in the Italian alder plantation was significantly more fertile, in terms of mineralisable nitrogen and extractable potassium, with associated higher pH and percentage of soil organic matter content. In the Italian alder plantation nitrogen, phosphorus and potassium were all positively correlated in a background fertility gradient across the plantation, which had apparently been unaffected by thinning treatment. Only phosphorus was higher in the Norway maple plantation, its distribution correlated with a potassium 'hotspot' in the central third of the plantation. Thinning treatment significantly raised soil organic matter contents in both plantations, but this soil variable was not found to have any significant influence on ground flora vegetation. Thinning treatment led to a significant increase in mineralisable nitrogen under a Norway maple canopy. Mineralisable nitrogen levels were much lower in the maple plantation than under Italian alder; and nitrogen was not a significant factor in field layer development in the maple plantation. The second PCA axis of variation in the Norway maple data represented a background pH gradient, which existed across the plantation. This pH gradient was associated with edge effects; the higher pH values occurring towards the north-eastern side of the plantation (Figure 3.7) and in the anomalous plot 6 (Figure 3.1). This plot has been most influenced by plantation edge effects, in terms of increased ride side light and higher disturbance levels due to thinning.

The successful establishment of the introduced ground flora species was less marked in the Italian alder plantation, due to the lack of potential germination niches and increased competition afforded by the more vigorous background vegetation. The establishment of most species was favoured by thinning in both plantations. Generally, the species best able to take advantage of conditions created by thinning were those more usually associated with higher light environments, e.g. *Scrophularia nodosa, Viola riviniana* and *Primula vulgaris*.

The first season results represent the establishment of introduced species into ground flora communities, while the second year represents niche consolidation by those species. Niche consolidation by certain species, such as *Silene dioica*, was so successful in the Norway maple plantation that other species which were slower to establish, e.g. *Milium effusum, Campanula trachelium* and *Bromopsis ramosa*, were favoured by niche availability in control rather than thinned plots. In the Italian alder plantation, where *Silene* was far less successful, *Bromopsis ramosa* and *Campanula trachelium* responded positively to thinning. The vigorous spontaneous vegetation under Italian alder, stimulated by thinning, provided too much shade / competition for *Silene* to dominate in thinned plots in this plantation. However, long term studies by Cohn (1994) suggested that early domination of ground flora communities by *Silene* is a positive sign for the future development of target communities. *Silene,* whose populations are likely to decline in later years, perhaps acts as a nurse species for slower developing species, such as *Hyacinthoides non-scripta* (see Section 6.7 on further work).

In the Norway maple plantation the introduced species came to dominate those ground flora communities into which their establishment was favoured by thinning. However, in the Italian alder plantation introductions did not dominate communities (except very locally), but formed an important component of ground flora communities. In both plantations, thinning treatment favoured establishment and niche consolidation by most introduced species.

The narrow window of treatment influence was compounded by edge effects, due to treatment plot size, experimental area and a limited buffer zone. Edge effects were, of course, not confined to the woodland light climate, but influenced other factors, e.g. the soil pH gradient in the Norway maple plantation. Although, edge effects clearly complicated results, the experiment is not so small that results were obscured by these effects.

This experiment supports the theory of Cohn (1994), that environmental conditions at the time of establishment are most important for the development of desirable ground flora communities. Cohn (1994) and other workers, such as Francis *et al.* (1992), found that once introduced species are established they compete well with spontaneous species. The more aggressive spontaneous vegetation in the Italian alder plantation is likely to diminish in vigour as the effects of the thinning treatment lessen, putting target woodland

species at a competitive advantage. Perhaps the increased edge effects impacting on a small experiment favour introduced woodland species in terms of earlier elimination of non-woodland competitors.

It is believed that certain species, such as *Urtica dioica*, can persist in dense shade if soil fertility is significantly high. Further information on the nutrient requirements of such species in light-stressed situations is needed (Section 6.7). Species like *Urtica* may occupy valuable niche space and provide competition for resources, but may also act as a surrogate canopy for introduced woodland herbs, ameliorating niche microclimates and perhaps enhancing their establishment. This hypothesis requires further investigation (Section 6.7).

It was hypothesised that light would be the major determinant of field layer establishment and early development in this experiment. It was postulated that light climate would not have such a large influence as to obscure identification of other important factors, with the aim of detecting more subtle fertility influences using CANOCO analyses. Although light was the major determinant of field layer vegetation in the Norway maple plantation, in the Italian alder plantation it was soil fertility, with light climate having a secondary influence. The fertility determinant in the Italian alder plantation was found to be background soil fertility, which had been apparently uninfluenced by thinning treatment. The hypothesised effect of thinning on mineralisable nitrogen, which occurred in the Norway maple plantation, may show in time in the Italian alder plantation, as the decay process accelerates in the cut tree stumps.

Light climate, as influenced by canopy thinning was found to be a major determinant of field layer development. Thinning created higher light climates, which favoured the establishment of the introduced species. However, the experiment also shows that canopy species was a major determinant of field layer development in secondary woodlands. The experiment suggests that, in the Italian alder plantation, soil fertility (i.e. trends in mineralisable nitrogen, potassium and phosphorus), as well as light climate, were correlated with the nature of the field layer vegetation. The experiment also indicates that the levels of fertility (at least for nitrogen) at which successful species introductions can be made were higher in woodland compared to grassland restoration schemes (Section 6.3). Although alders are perhaps an extreme example of canopy influencing soil characteristics, and it is still likely that in most stands it is canopy

architecture influencing the light climate which is the major determinant of field layer characteristics.

3.5 Conclusions

- Woodland ground flora can be successfully introduced into existing planted Norway maple and Italian alder communities, without use of a herbicide pretreatment and into relatively vigorous established vegetation.

- Canopy thinning, by 50% prior to establishment, significantly enhanced the success of the introduced species in both plantations. The thinning increased dark phase PAR from less than 10% full daylight to 15-20% and light phase PAR from 60% to 68% one year after thinning.

- The presence of a relatively open field layer community prior to species introductions enhanced the success of the introduced species in the Norway maple plantation. There is some evidence to suggest that thinning created a recipient vegetation more favourable to subsequent introductions. The relative importance of the higher light regime and the disturbance associated with thinning in enhancing success of the introduced species is uncertain.

- An inherent fertility gradient (in nitrogen, potassium and phosphorus) represented the most major trend in the Italian alder plantation, which affected ground flora establishment.

- Thinning still had a positive influence on ground flora introductions, even when the light climate exerted a secondary effect on the vegetation. Therefore, depending on initial canopy density, thinning is likely to be an extremely useful management tool when attempting to maximise success of ground flora enhancement.

- A balance between thinning treatment and associated edge effects needs to be struck in small plots. Plantation edge effects may encourage the initial establishment of introduced species, but their persistence in the longer term, at the woodland edge, is unlikely to be favoured. However, some treatment plot edge effects, especially where treatment plots are small, will enhance species establishment, and favour their persistence, with the subsequent accelerated reduction in treatment influence.

- Bryophytes appeared to play an important role in niche microclimate amelioration, which enhanced success of introduced species in the Norway maple plantation. The apparent negative impact of thinning operations on this vegetation parameter should be noted.

- Canopy species, and its influence on environmental conditions, was the major determinant of field layer development in this experiment. The effect of the canopy architecture of the Norway maple on the light climate and the influence on soil fertility of the nitrogen fixing capabilities of the Italian alder produced the overriding effects on vegetation in this experiment. However, woodland habitat creation / restoration programmes would more usually be dealing with a native, broad-leaved, mixed canopy, which more closely resemble target communities. In a mixed secondary woodland it would be expected that the influence of tree species would be diluted. This scenario has been investigated in Experiment 2, which was also designed to minimise edge effects, so apparent in the current experiment.

Figure 3.1 Layout of Experiment 1: the light manipulation experiment at the Wolverhampton Environment Centre. The relative position of the two species stands is illustrated. Treatment plot and quadrat locations are shown.

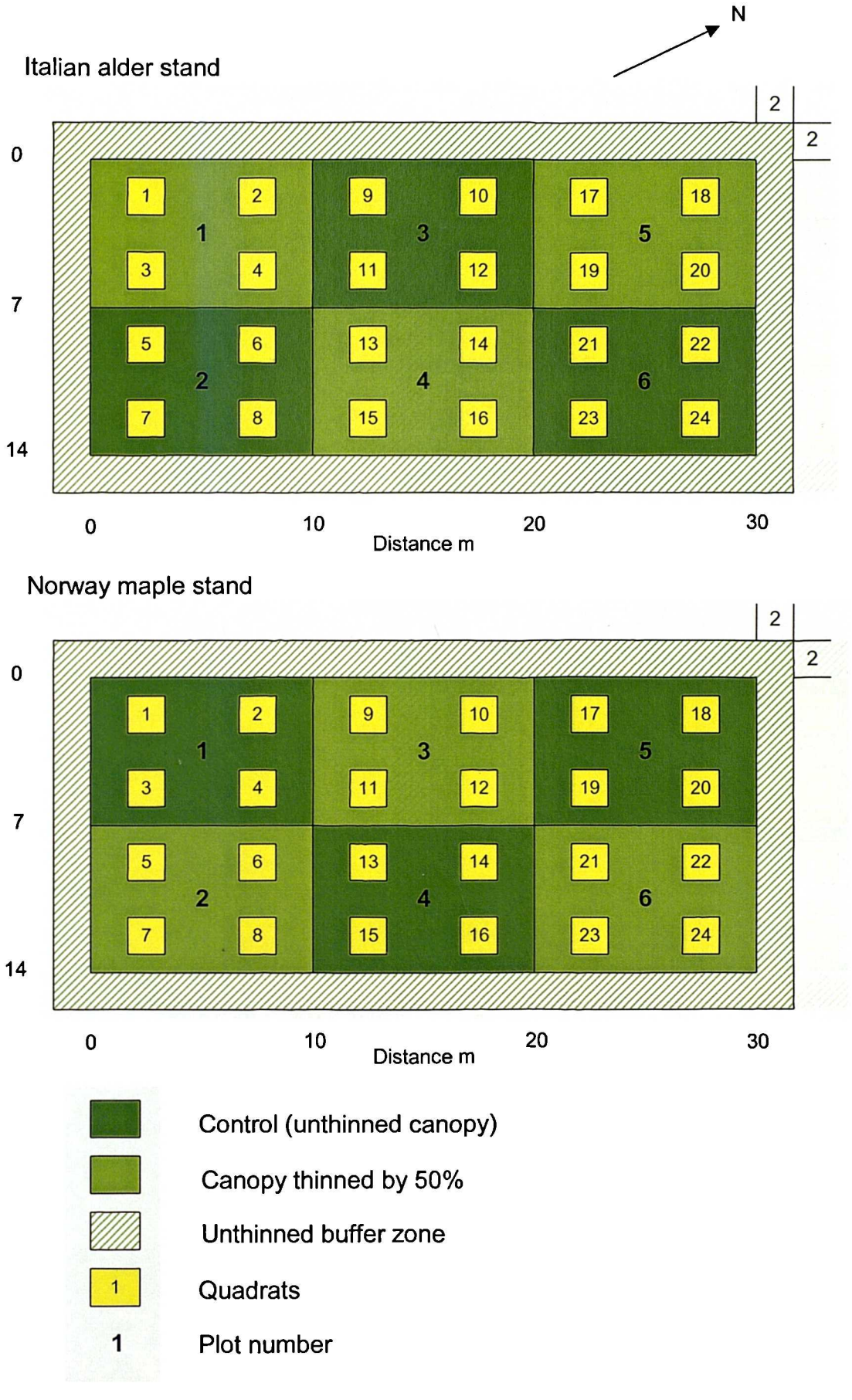


Plate 3.1 The Norway maple stand of Experiment 1 on establishment, 18/03/98, as seen from thinned plot 6, looking into control plots 4 and 5. The spontaneous field layer is a sparse vegetation where tree seedlings and bryophytes predominate.

Plate 3.2 The Italian alder stand of Experiment 1 at establishment, on 18/03/98, looking from thinned plot 4 into control plots 2 and 3. The spontaneous field layer comprises a more vigorous vegetation consisting of aggressive woodland and ruderal species.

Plate 3.3 First season (13/09/98) vegetation response in the Norway maple stand of Experiment 1, looking from the corner of thinned plot 2 into control plot 1 and thinned plot 3 beyond. Introduced species, such as *Silene dioica* and *Scrophularia nodosa,* are prominent features of the vegetation. A stark contrast in the vegetation is evident at treatment plot boundaries.

Plate 3.4 First season (13/09/98) vegetation response in the Italian alder stand of Experiment 1, as seen from thinned plot 4, with control plot 6 in the background. Introduced species are a less prominent feature of the vegetation than in the Norway maple stand and treatment plot boundaries are discernable, but less marked.

Plate 3.5 Detail of second season (15/06/99) vegetation response in the Norway maple stand of Experiment 1, under a thinned canopy in plot 3. This tall herb community is characterised by introduced species. *Silene dioica* dominates with abundant *Scrophularia nodosa* and *Brachypodium sylvaticum*.

Plate 3.6 Second season (15/06/99) vegetation response in the Norway maple stand of Experiment 1. Treatment differences are clearly evident in comparison with the barren control plot 5 in the forground and the tall herb community in the thinned plot 3 behind. The abrupt interfaces between light treatments on the ground are not visible in the canopy.

Plate 3.7 Detail of second season (15/06/99) vegetation response in the Italian alder stand of Experiment 1, under a thinned canopy, in plot 1. This tall herb community is characterised, but not dominated by, introduced species. *Silene dioica* and *Bromopsis ramosa* are locally abundant with frequent *Scrophularia nodosa* and *Brachypodium sylvaticum*.

Plate 3.8 Second season (15/06/99) vegetation response in the Italian alder stand of Experiment 1, in a control plot, 6. This tall herb community is characterised by aggressive woodland and ruderal species, such as *Rubus fruticosus*, *Geum urbanum* and willowherbs, with only the occasional occurrence of introduced species.

Figure 3.2 Contour map of Photosynthetically Active Radiation (expressed as a percentage of ambient PAR levels) reaching the field layer in the two species stands of Experiment 1, during the woodland dark phase in 1999.

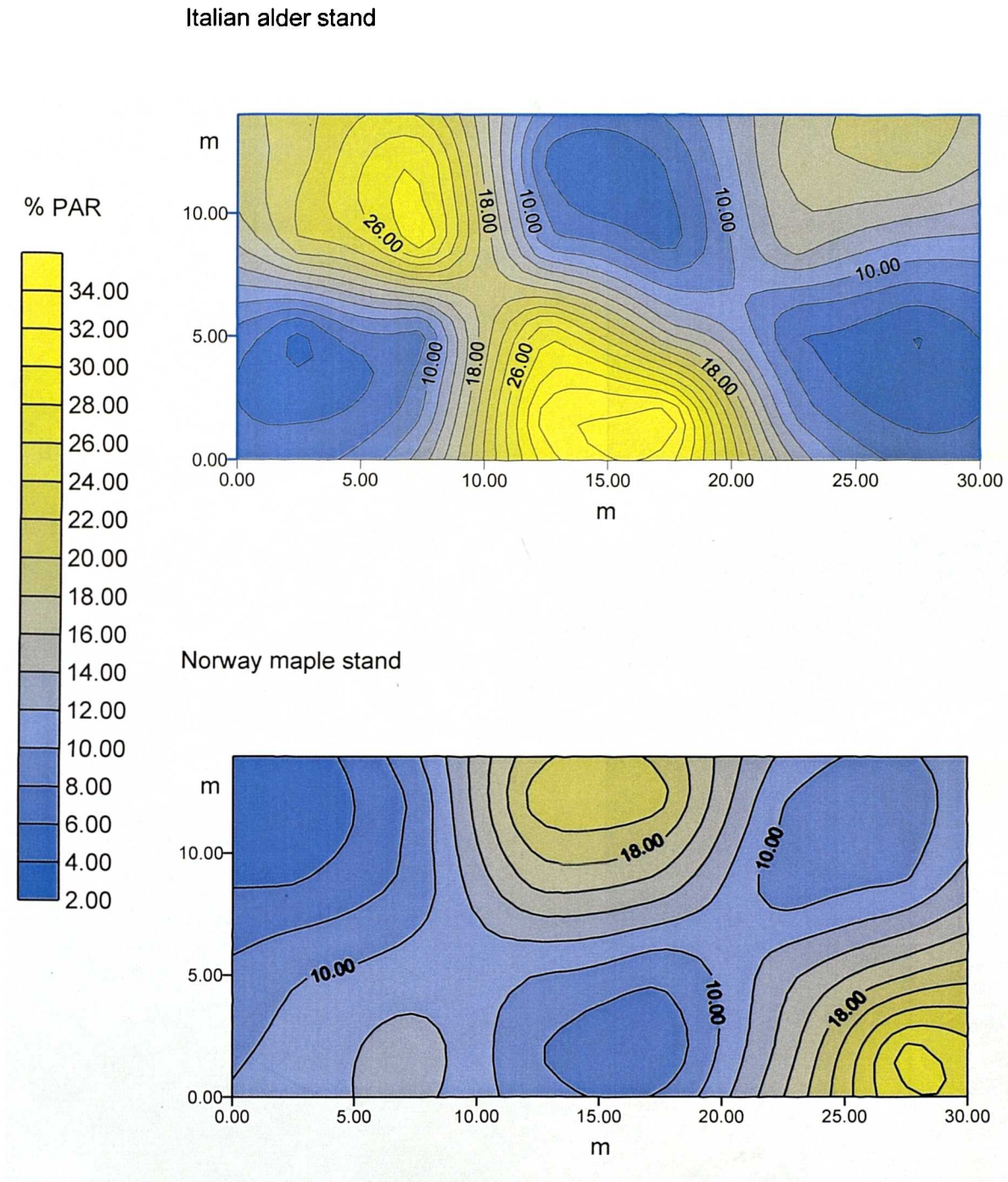


Figure 3.3 Contour map of Photosynthetically Active Radiation (expressed as a percentage of ambient PAR levels) reaching the field layer in the two species stands of Experiment 1, during the woodland light phase in 1999.

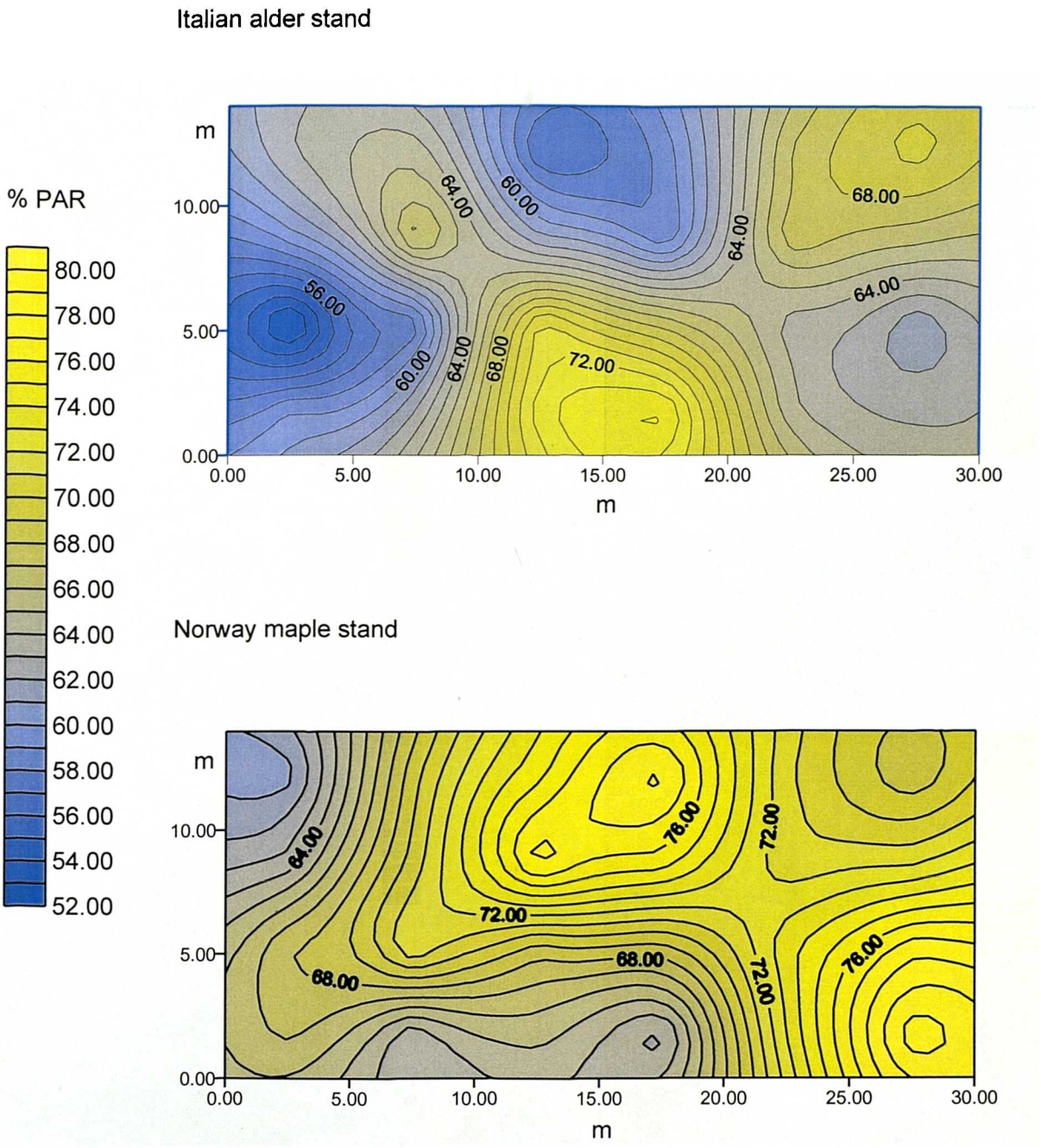


Figure 3.4 Contour map of mineralisable nitrogen (mg kg-1) occurring across the two species stands of Experiment 1 in 1999.

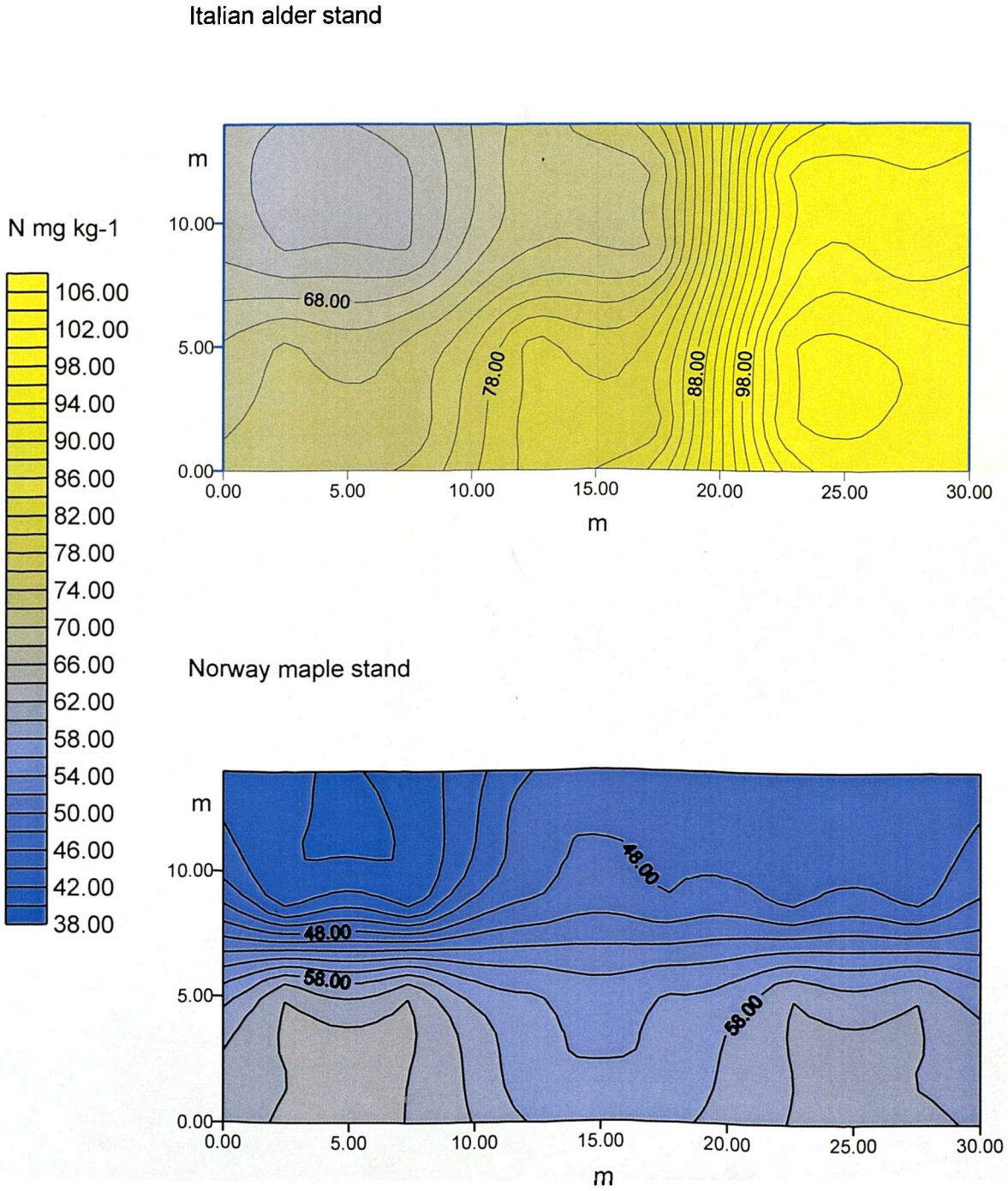


Figure 3.5 Contour map of extractable potassium (mg kg-1) occurring across the two species stands of Experiment 1 in 1999.

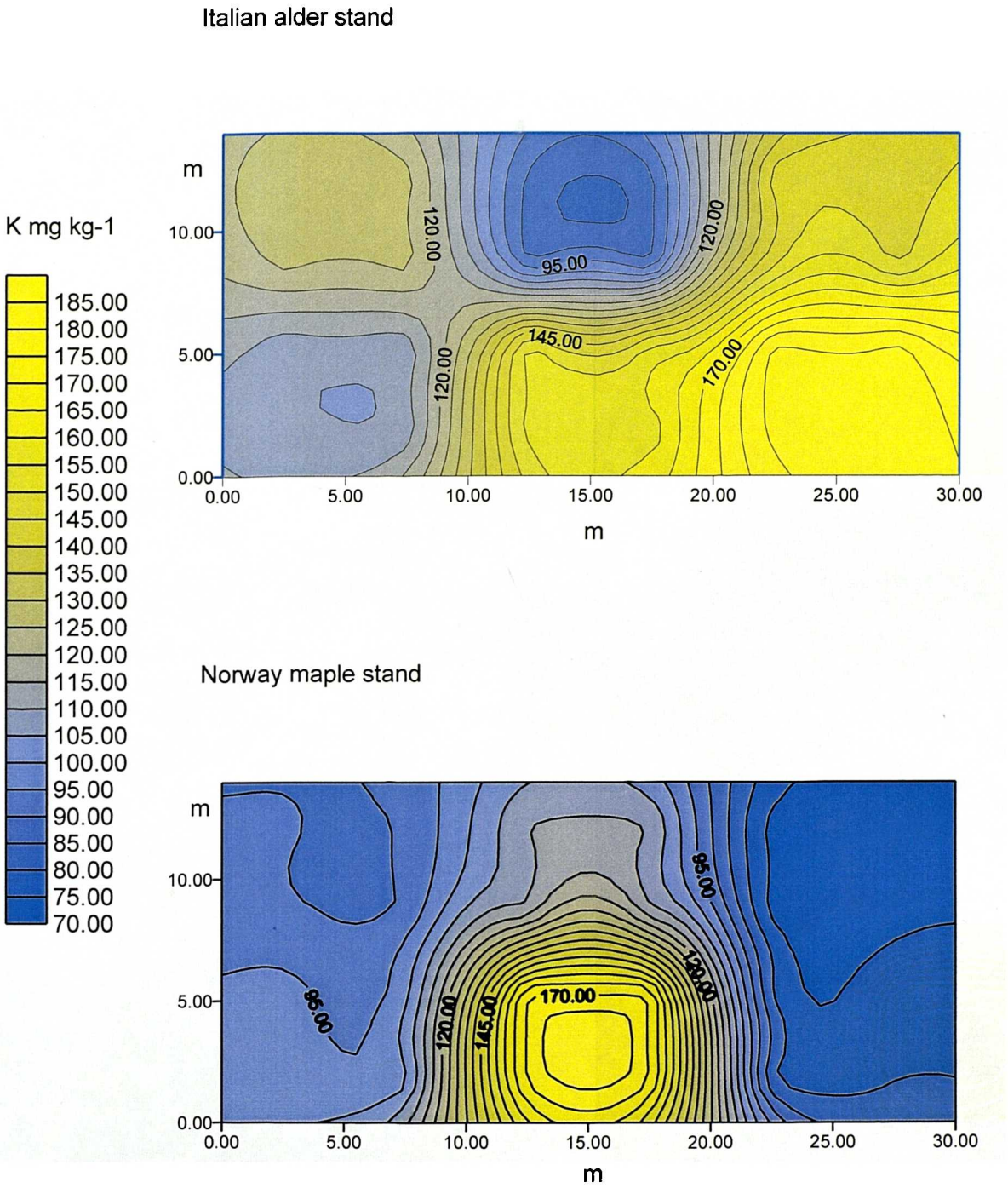


Figure 3.6 Contour map of extractable phosphorus (mg kg-1) occurring across the two species stands of Experiment 1 in 1999.

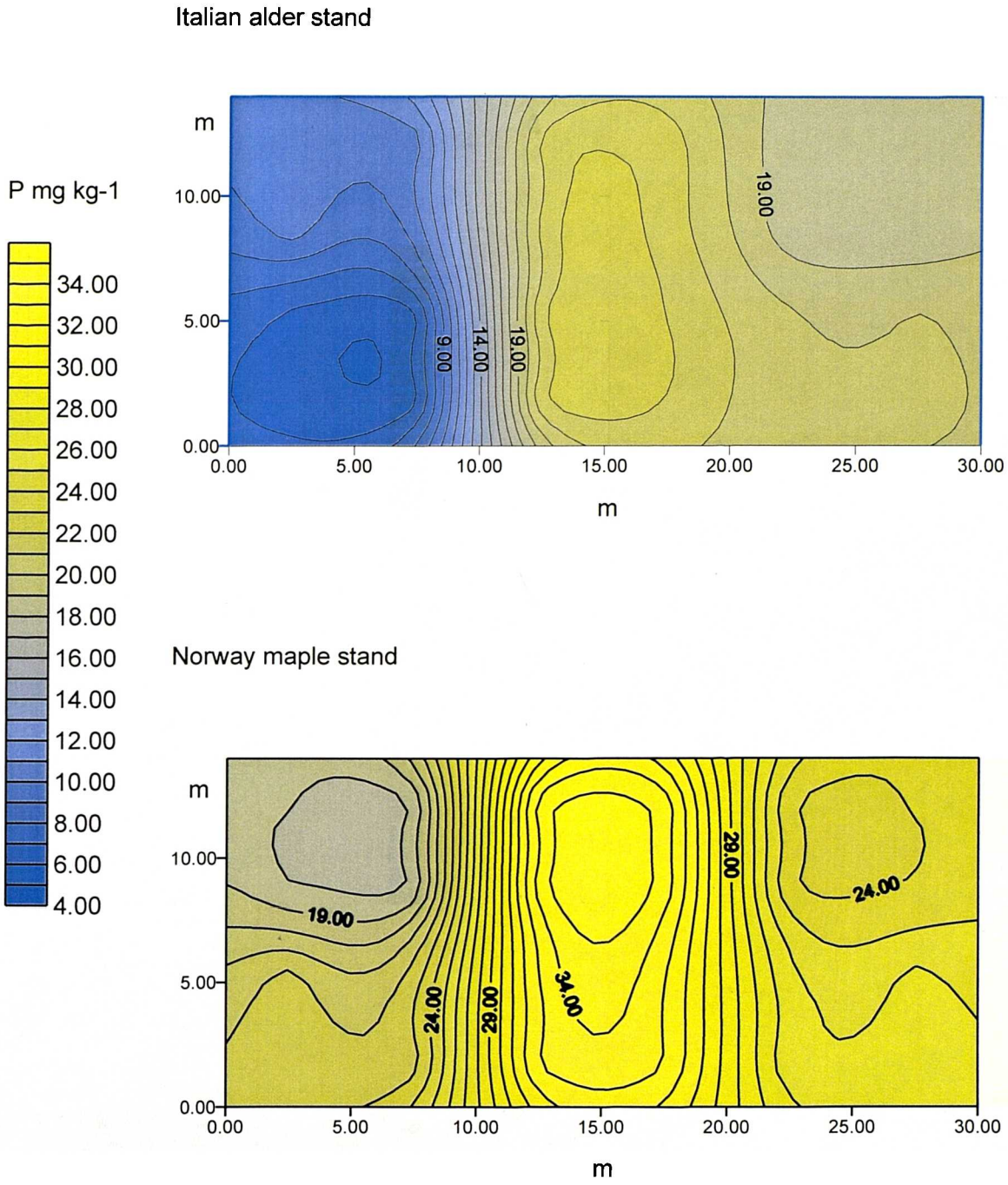


Figure 3.7 Contour map of soil pH values occurring across the two species stands of Experiment 1 in 1999.

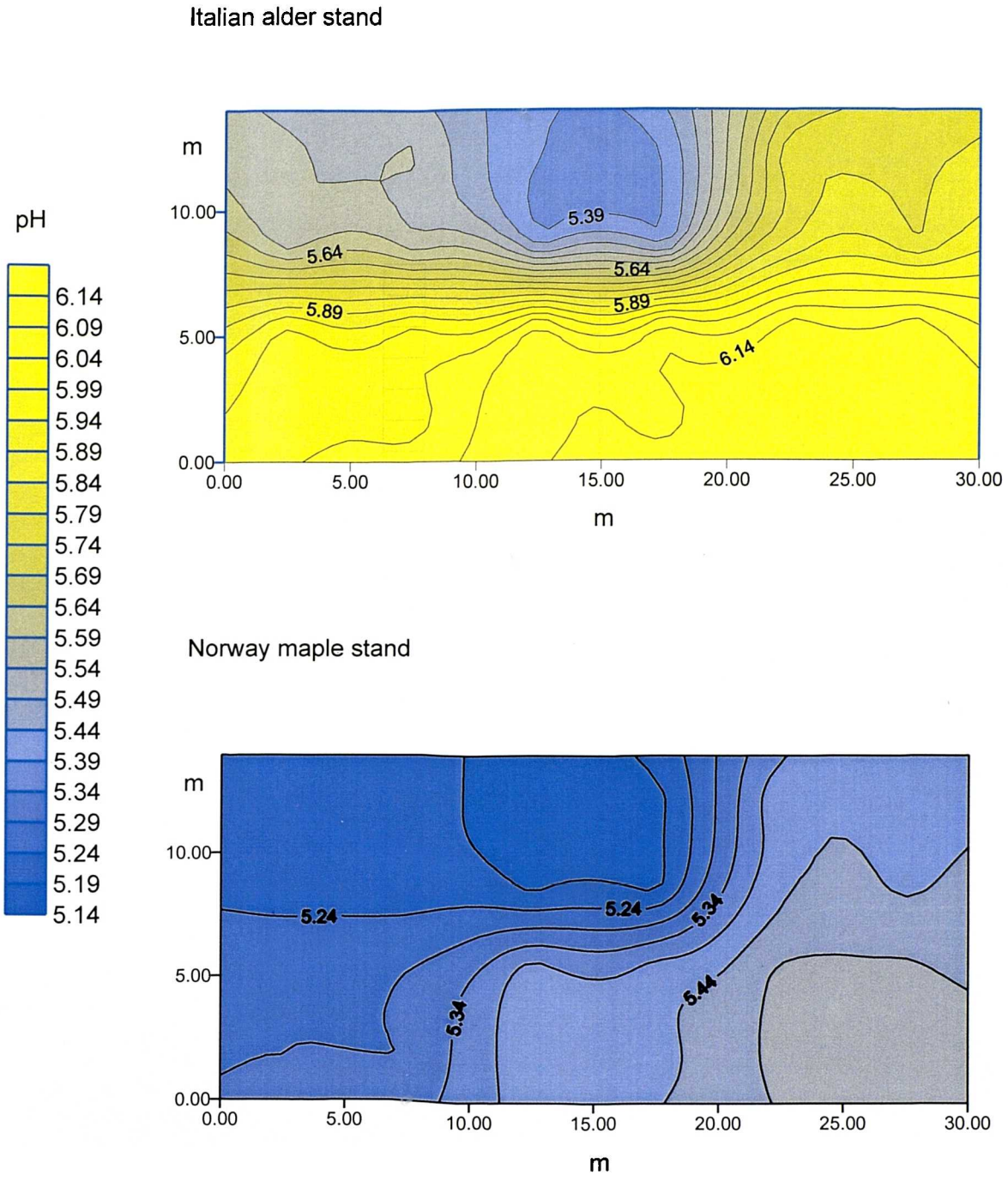


Figure 3.8 Contour map showing percentage cover of bryophytes occurring across the two species stands of Experiment 1 in 1999.

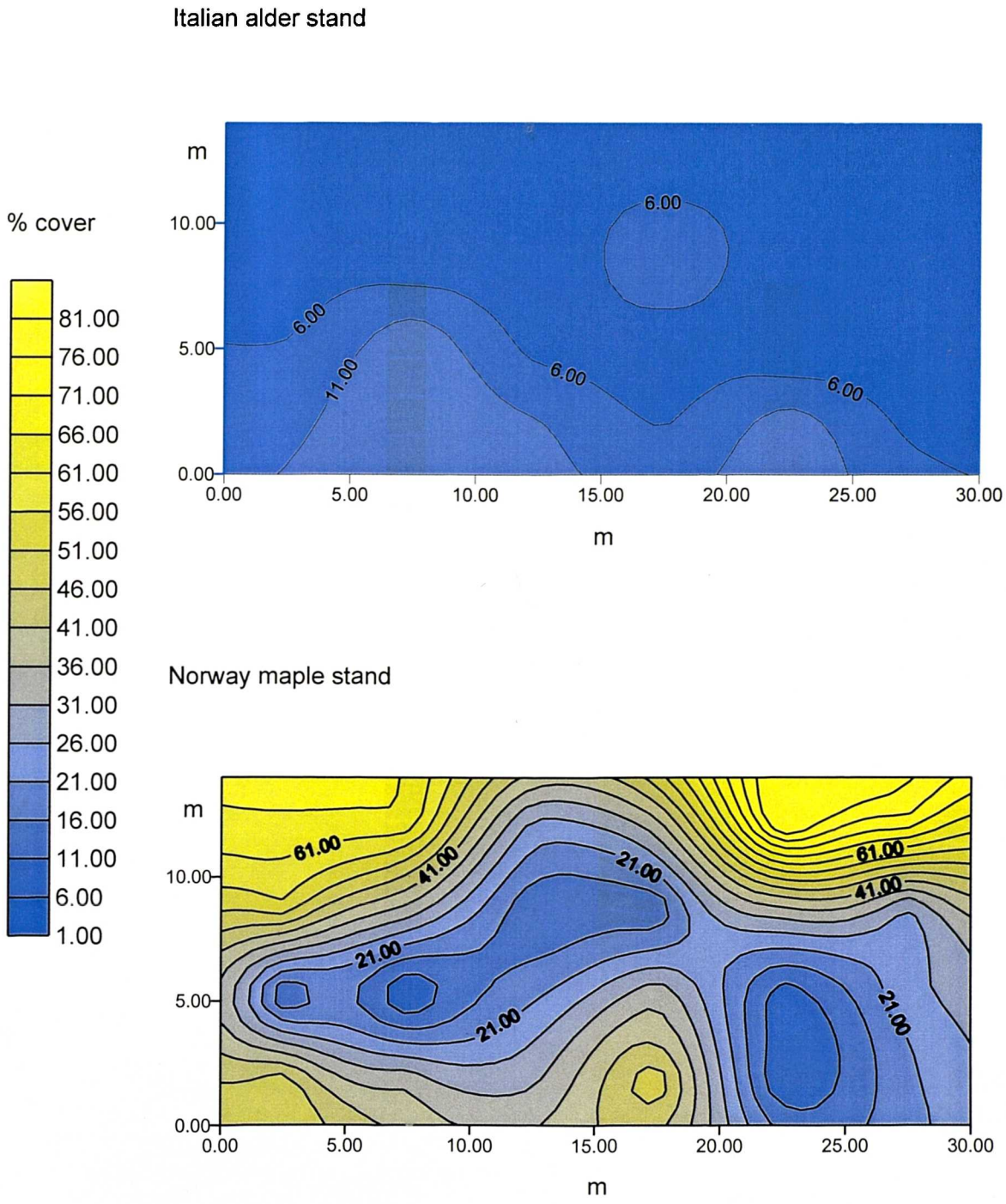


Table 3.1: Table of Means of treatment significant variables in Experiment 1.

Norway Maple

Test statistic and significance level with means and SEs per light treatment

Light treatment	PARD	SE	PARL	SE	Canopy 98	SE
t value	- 4.95	***	- 3.15	***	7.48	***
Thinned	15.9	1.49	73.4	1.49	52.2	5.55
Unthinned	8.1	0.54	67.6	1.09	94.5	1.14

Test statistic and significance level with means and SEs per light treatment

Light treatment	Canopy 99	SE	Litter 98	SE	Bryophyte 99	SE
t value	6.7	***	2.41	*	3.74	***
Thinned	70.4	2.63	24.2	2.81	20.3	4.08
Unthinned	94.9	1.56	34.6	3.28	48.3	6.32

Test statistic and significance level with means and SEs per light treatment

Light treatment	min N	SE	OM	SE	Axis1 98 t	SE
t value	- 3.26	**	-5.53	***	-4.68	***
Thinned	56.6	1.85	7.3	0.05	2.57	0.27
Unthinned	48.0	1.90	7.0	0.03	1.15	0.13

Test statistic and significance level with means and SEs per light treatment

Light treatment	Axis1 99 t	SE
t value	4.01	***
Thinned	1.01	0.19
Unthinned	2.31	0.26

Italian alder

Test statistic and significance level with means and SEs per light treatment

Light treatment	PARD	SE	PARL	SE	Canopy 98	SE
t value	- 7.04	***	- 5.06	***	6.57	***
Thinned	23.0	2.28	67.6	1.17	54.2	4.52
Unthinned	6.3	0.62	59.6	1.06	85.7	1.60

Test statistic and significance level with means and SEs per light treatment

Light treatment	Canopy 99	SE	Bareground 98	SE	Litter 98	SE
t value	4.69	***	3.16	**	6.05	***
Thinned	43.5	7.40	4.5	0.87	9.3	1.71
Unthinned	82.4	3.75	10.6	1.72	30.3	3.03

Test statistic and significance level with means and SEs per light treatment

Light treatment	OM	SE	Axis2 98 t	SE	Axis2 99 t	SE
t value	-3.16	**	1.73	*	2.92	**
Thinned	8.2	0.14	1.32	0.3	1.22	0.24
Unthinned	7.7	0.06	2.02	0.26	2.28	0.27

df = 22. t Critical one-tail = 1.72 t Critical two-tail = 2.07 SE = standard error.

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively.

t: t-test performed on transformed data. 98/99: year. OM: soil organic matter (%).

Table 3.2: Table of Means of plantation significant variables in Experiment 1.

	Test statistic and signifcance level with means and SEs per plantation					
Plantation	PARL	SE	Canopy 99t	SE	Litter 98	SE
t value	4.39	***	3.14	**	2.64	**
Norway Maple	70.5	1.09	82.7	2.61	29.4	2.38
Italian alder	63.6	1.14	63.0	3.75	19.8	2.77

	Test statistic and signifcance level with means and SEs per plantation					
Plantation	Litter 99t	SE	Bareground 98t	SE	Bareground 99t	SE
t value	13.34	***	-5.22	***	-3.17	**
Norway Maple	37.5	1.80	2.1	0.49	3.25	0.04
Italian alder	4.4	0.73	7.5	1.23	8.25	0.15

	Test statistic and signifcance level with means and SEs per plantation					
Plantation	Bryophyte 98t	SE	Bryophyte 99t	SE	pH	SE
t value	15.14	***	6.76	***	-7.81	***
Norway Maple	71.9	1.66	34.3	3.08	5.3	0.03
Italian alder	13.6	1.91	5.6	1.14	5.8	0.06

	Test statistic and signifcance level with means and SEs per plantation					
Plantation	min N	SE	Ext Kt	SE	Ext P	SE
t value	- 8.52	***	- 3.62	***	5.78	***
Norway Maple	52.3	1.58	103.8	0.02	26.4	1.21
Italian alder	82.5	3.17	135.8	0.02	16.2	1.30

	Test statistic and signifcance level with means and SEs per plantation					
Plantation	OM	SE	Den Intro 98	SE	Den Intro 99	SE
t value	-7.42	***	7.28	***	7.54	***
Norway Maple	7.2	0.05	129.3	11.32	127.9	8.75
Italian alder	7.9	0.09	36.8	5.78	44.0	6.89

df = 46. t Critical one-tail = 1.68 t Critical two-tail = 2.01 SE = standard error.

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively.

t: t-test performed on transformed data. 98/99: year. OM: soil organic matter (%).

Den Intro: density of introduced species.

Figure 3.9 Mean cover abundance of introduced and spontaneous species occurring in thinned and unthinned plots in the Norway maple plantation of Experiment 1, in (a) 1998 and (b) 1999. Letters denote significant difference between means ($p < 0.05$).

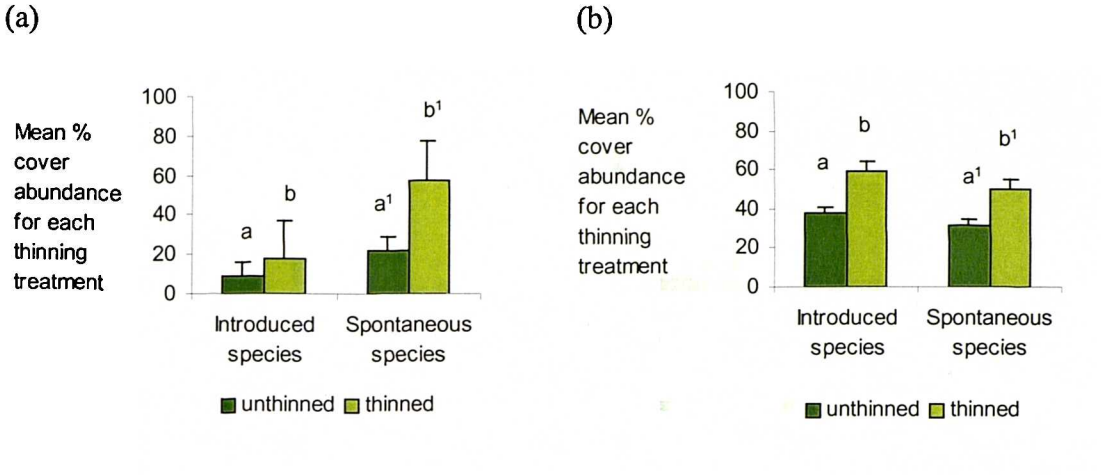
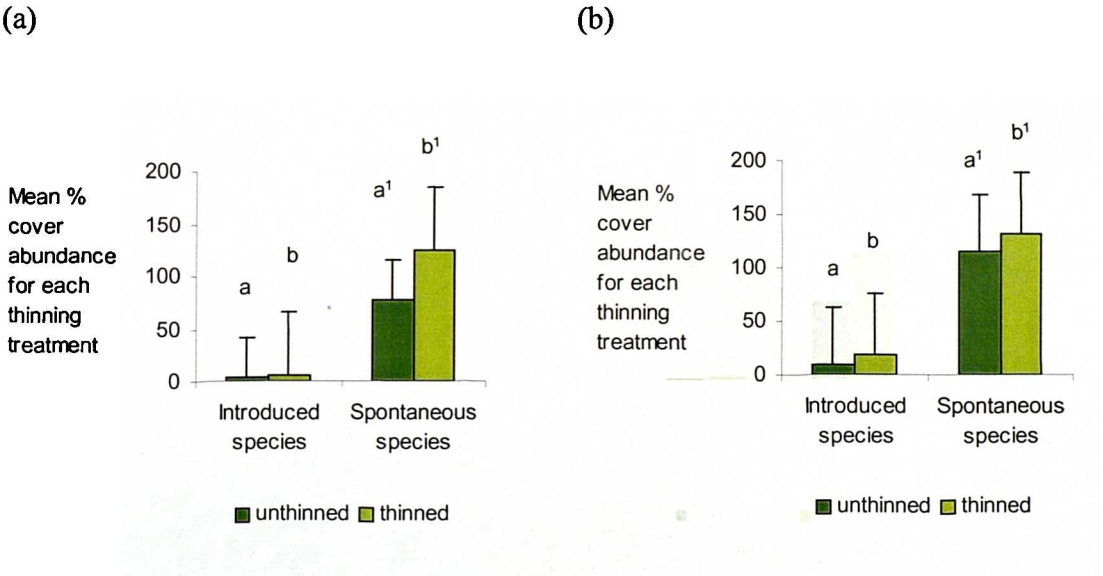


Figure 3.10 Mean cover abundance of introduced and spontaneous species occurring in thinned and unthinned plots in the Italian alder plantation of Experiment 1, in (a) 1998 and (b) 1999. Letters denote significant difference between means ($p < 0.05$).



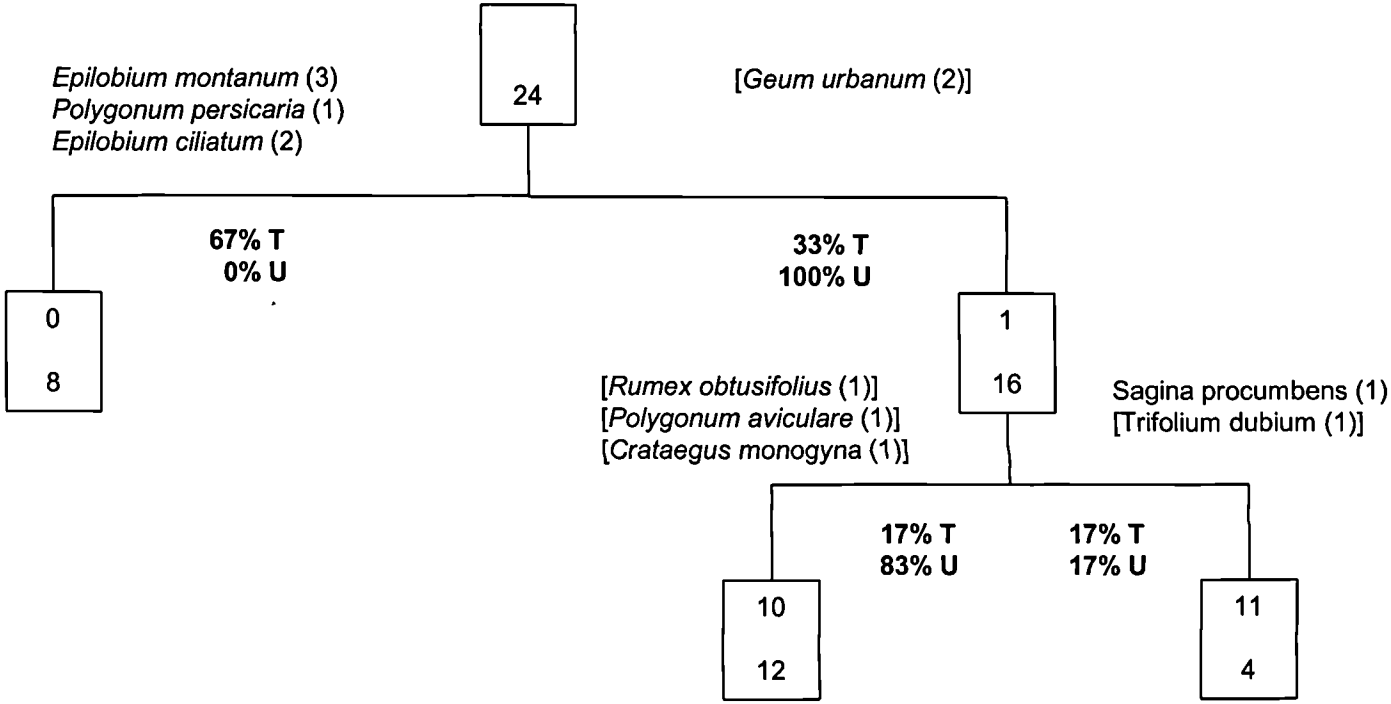


Figure 3.11
experiment at the Wolverhampton Environment Centre). The upper figure in each box indicates the TWINSPAN group, the lower figure, the number of samples in each group. Indicator species are listed in order of importance with pseudospecies levels in brackets to indicate abundance. Preferential species, denoted by square brackets, are also given in order of importance with pseudospecies level in brackets. Bold numbers indicate the percentage of samples from thinned (**T**) and unthinned (**U**) treatment plots assigned to the negative (left hand) or the positive (right hand) group. Introduced species are shown in bold.

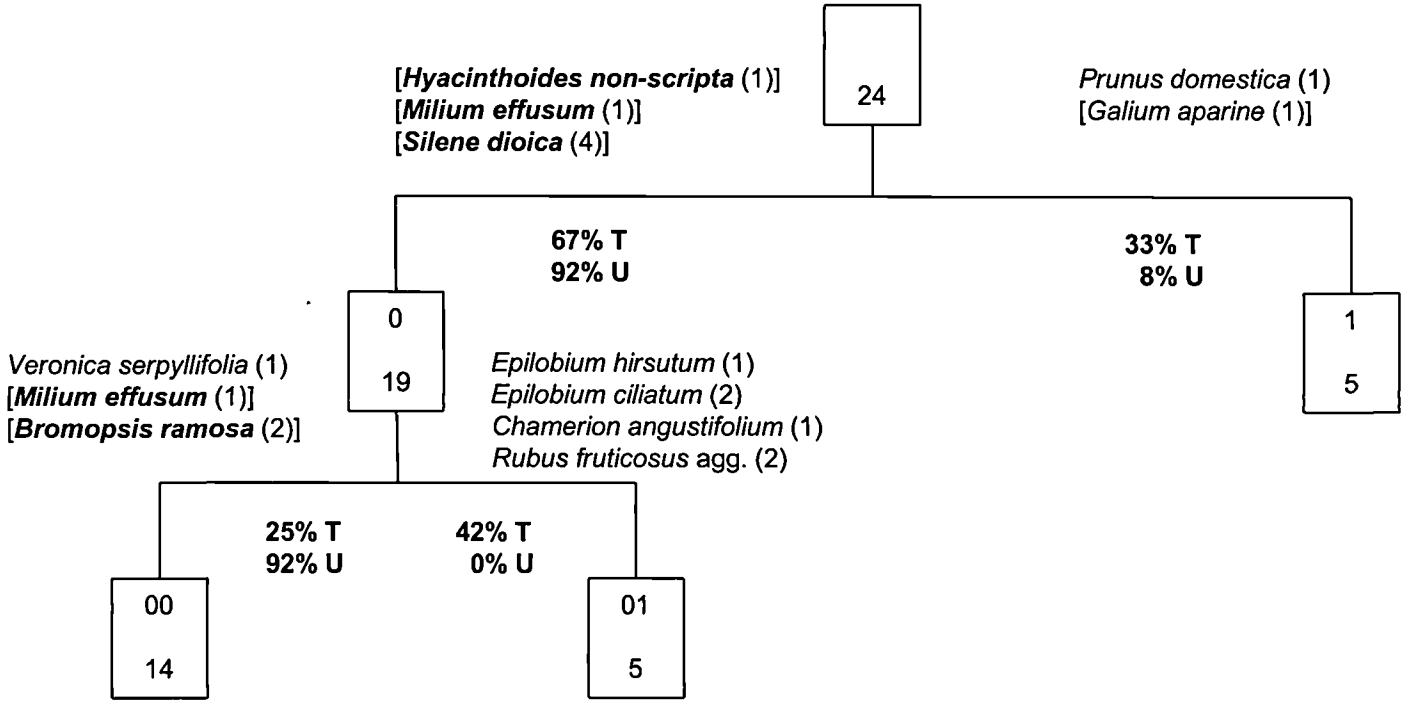


Figure 3.12 TWINSPAN classification of the 1999 vegetation data from the Norway maple stand of Experiment 1 (the light manipulation experiment at the Wolverhampton Environment Centre). The upper figure in each box indicates the TWINSPAN group, the lower figure, the number of samples in each group. Indicator species are listed in order of importance with pseudospecies levels in brackets to indicate abundance. Preferential species, denoted by square brackets, are also given in order of importance with pseudospecies level in brackets. Bold numbers indicate the percentage of samples from thinned (**T**) and unthinned (**U**) treatment plots assigned to the negative (left hand) or the positive (right hand) group. Introduced species are shown in bold.

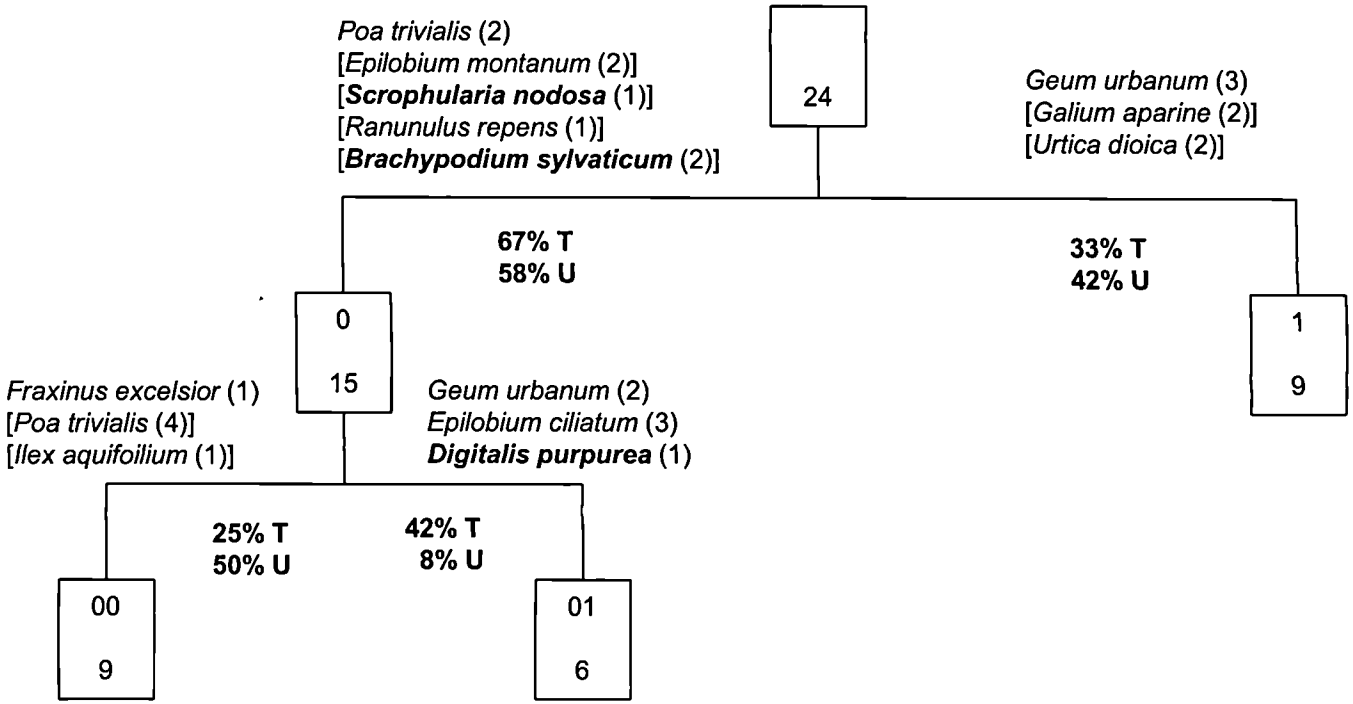


Figure 3.13 TWINSPAN classification of the 1998 vegetation data from the Italian alder stand of Experiment 1 (the light manipulation experiment at the Wolverhampton Environment Centre). The upper figure in each box indicates the TWINSPAN group, the lower figure, the number of samples in each group. Indicator species are listed in order of importance with pseudospecies levels in brackets to indicate abundance. Preferential species, denoted by square brackets, are also given in order of importance with pseudospecies level in brackets. Bold numbers indicate the percentage of samples from thinned (**T**) and unthinned (**U**) treatment plots assigned to the negative (left hand) or the positive (right hand) group. Introduced species are shown in bold.

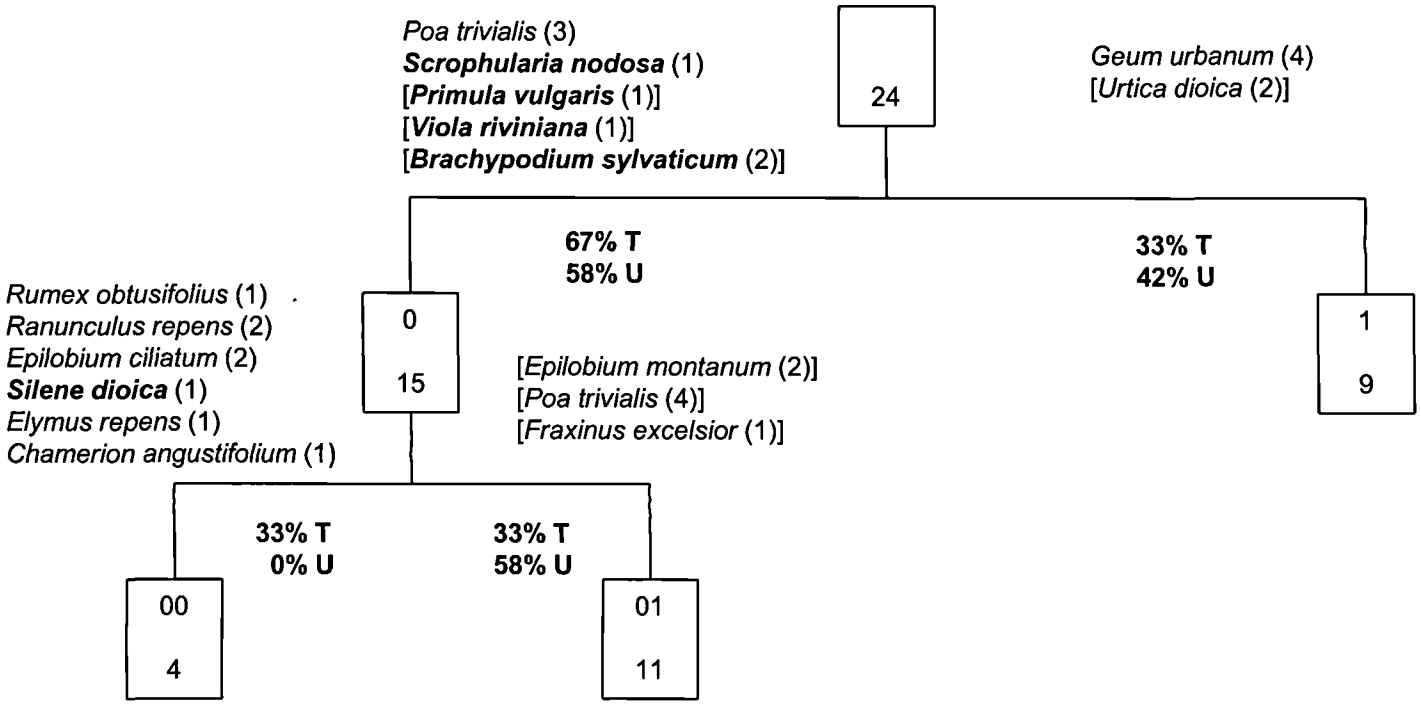
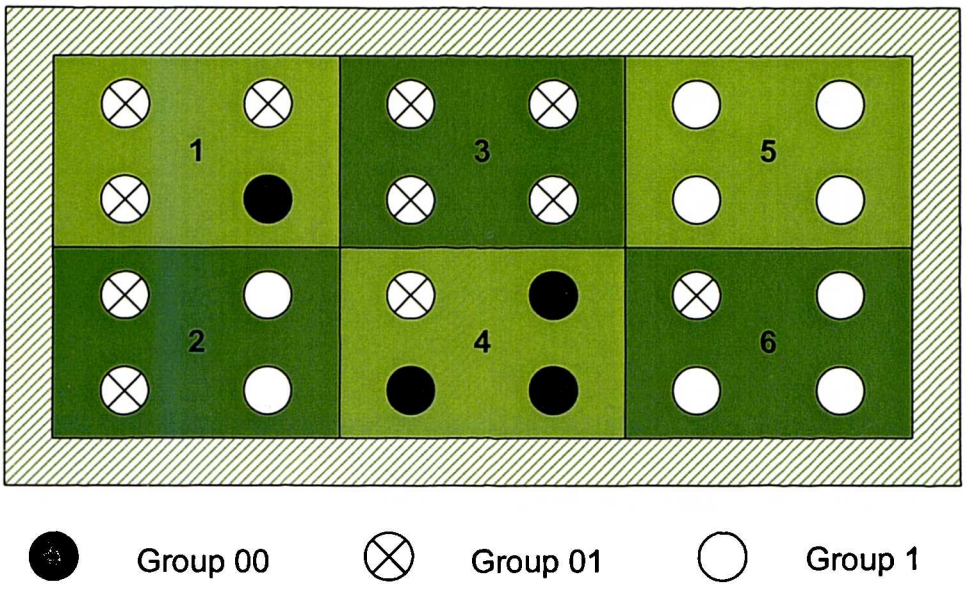


Figure 3.14 TWINSPAN classification of the 1999 vegetation data from the Italian alder stand of Experiment 1 (the light manipulation experiment at the Wolverhampton Environment Centre). The upper figure in each box indicates the TWINSPAN group, the lower figure, the number of samples in each group. Indicator species are listed in order of importance with pseudospecies levels in brackets to indicate abundance. Preferential species, denoted by square brackets, are also given in order of importance with pseudospecies level in brackets. Bold numbers indicate the percentage of samples from thinned (**T**) and unthinned (**U**) treatment plots assigned to the negative (left hand) or the positive (right hand) group. Introduced species are shown in bold.

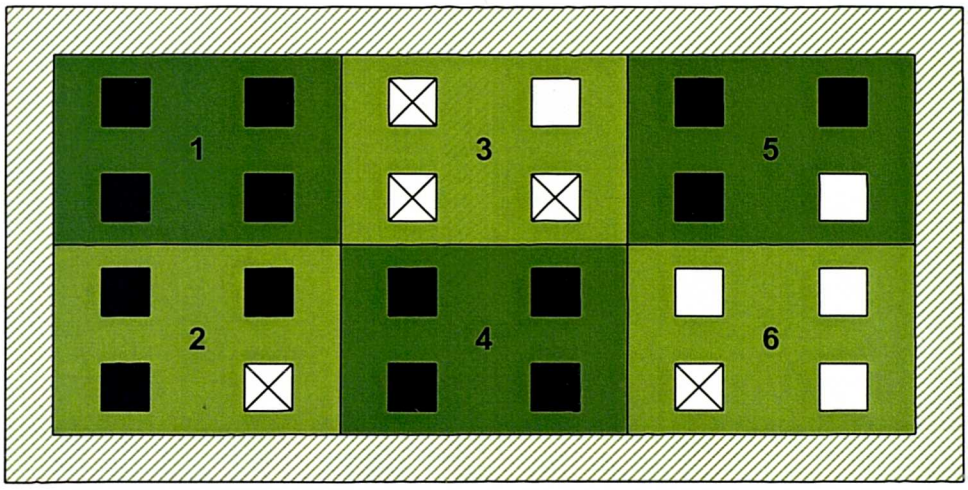
Figure 3.15 Location map of samples recorded in 1999 assigned to TWINSPAN end groups. Treatment plot position is shown.

Italian alder stand



Group 00 Group 01 Group 1

Norway maple stand



Group 00 Group 01 Group 1

Control (unthinned canopy) Unthinned buffer zone

Canopy thinned by 50% 1 Plot number

Table 3.3: Environmental variables which were significant under the Monte Carlo permutation testing during manual selection in RDA. (permutation number = 199).

Vegetation dataset analysed	Variable	F value	p-value estimate
Norway maple 1998	thinning treatment	4.277	0.01 **
	bryophytes	2.602	0.005 **

Significant variables explain 25.5% of species variance out of 37.3%, which represents the species variance explained if all measured variables had been included in the model.

Norway maple 1999	bryophytes	4.458	0.005 **
	pH	2.776	0.005 **
	Dark phase PAR	2.586	0.005 **

Significant variables explain 35.5% of species variance out of 65%, which represents the species variance explained if all measured variables had been included in the model.

Italian alder 1998	thinning treatment	2.171	0.05 *

Significant variables explain 9% of species variance out of 27.8%, which represents the species variance explained if all measured variables had been included in the model.

Italian alder 1999	Mineralisable nitrogen	6.24	0.005 **
	Extractable phosphorus	3.584	0.01 **
	Extractable potassium	2.858	0.015 *
	Light phase PAR	1.903	0.05 *

Significant variables explain 47.1% of species variance out of 75.4%, which represents the species variance explained if all measured variables had been included in the model.

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively.

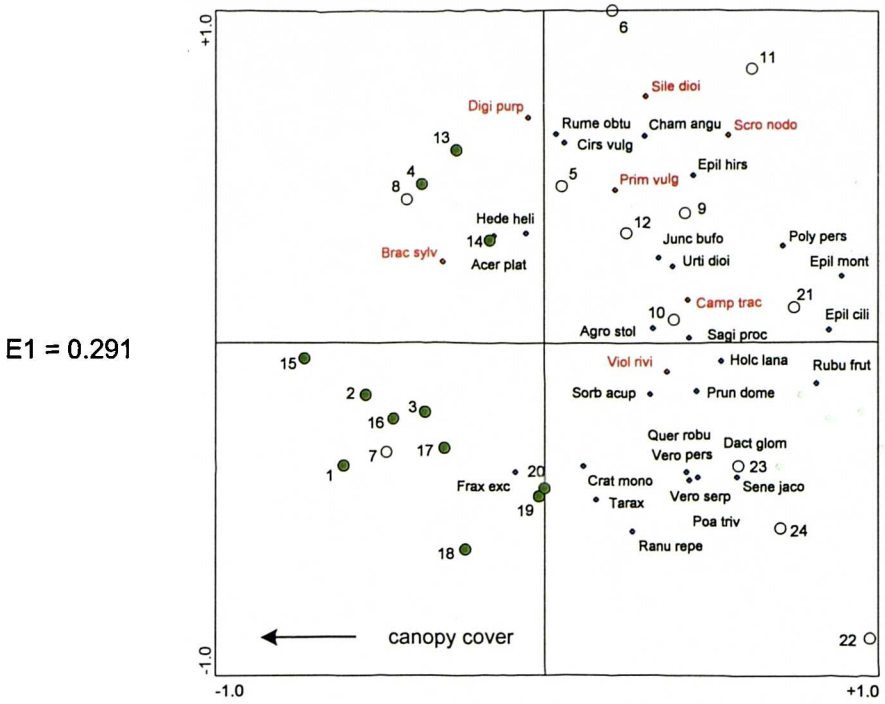


Figure 3.16 Species and sample scatter plot of the first two axes from PCA on the 1998 Norway maple vegetation data. Light treatments are colour coded, as are introduced and spontaneous species (see Figure 3.15 for key). $\lambda 1$ = 29.1% of species variance; $\lambda 1 + \lambda 2$ = 42.5% of species variance.

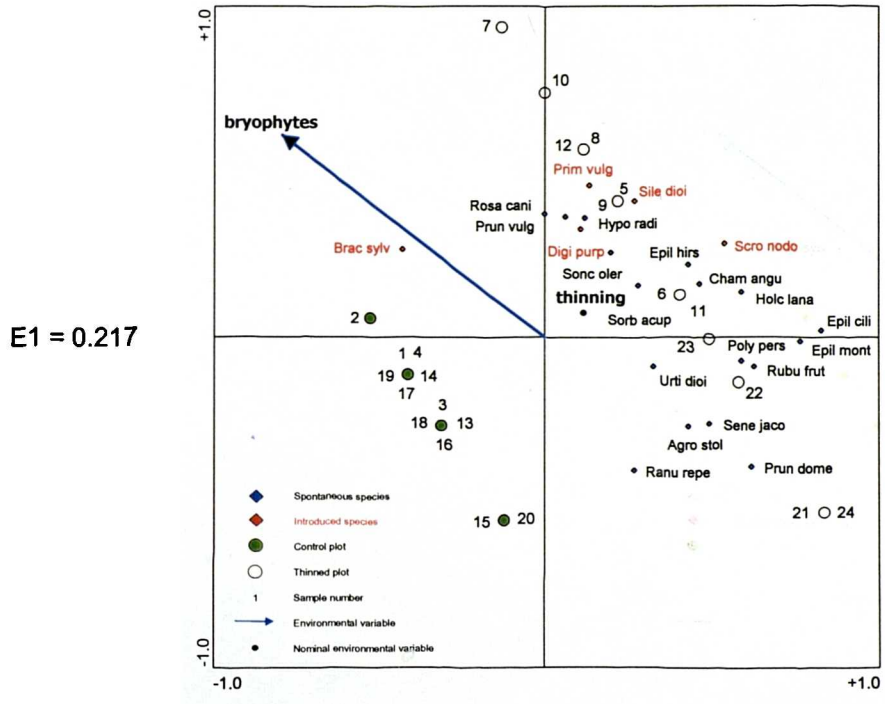
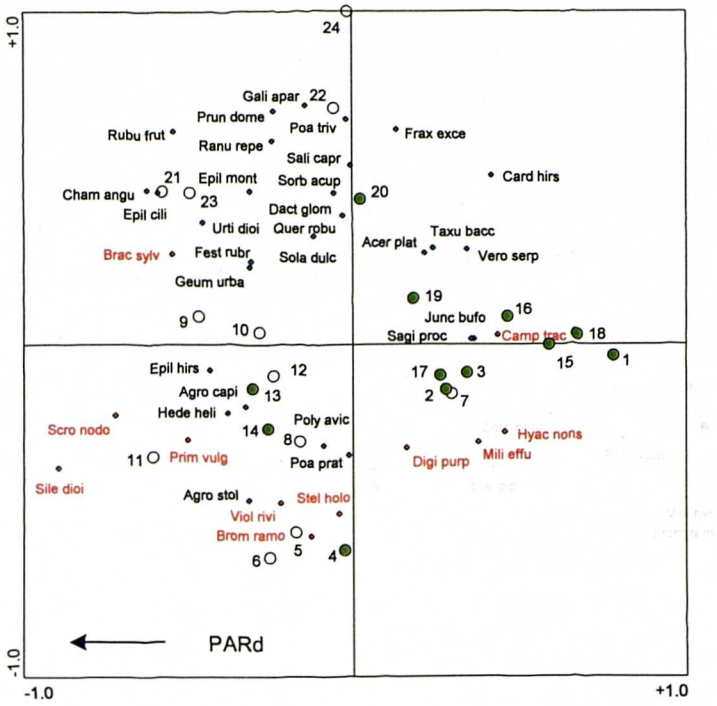


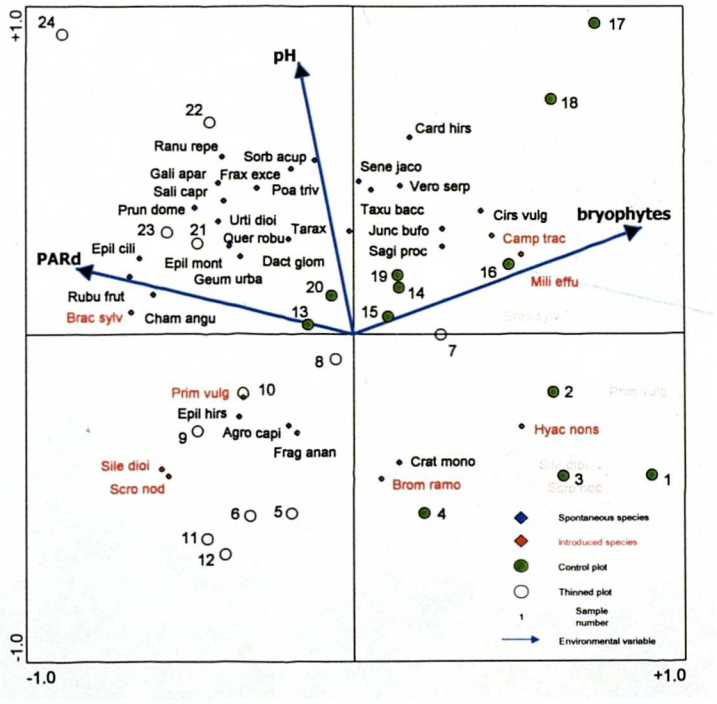
Figure 3.17 RDA Triplot of species, samples and significant environmental variables for the 1998 Norway maple vegetation data. Light treatments are colour coded, as are introduced and spontaneous species.
$\lambda 1$ = 21.7% of species variance = 85.2% of species-environment relation.
$\lambda 1 + \lambda 2$ = 25.5% of species variance = 100% of species-environment relation.
All axes are significant and the sum of all canonical eigenvalues is 0.255.



E1 = 0.266

E2 = 0.194

Figure 3.18 Species and sample scatter plot of the first two PCA axes from the 1999 Norway maple vegetation data. Samples are colour coded according to light treatment and species according to their origin (see Figure 3.17 for key). $\lambda 1$ = 26.6% of species variance; $\lambda 1 + \lambda 2$ = 46% of species variance.



E1 = 0.200

E2 = 0.120

Figure 3.19 RDA Triplot of species, samples and significant environmental variables for the 1999 Norway maple vegetation data. Samples are colour coded according to light treatment and species according to their origin.
$\lambda 1$ = 20% of species variance = 57.1% of species-environment relation.
$\lambda 1 + \lambda 2$ = 31.9% of species variance = 91.3% of species-environment relation.
All axes are significant and the sum of all canonical eigenvalues is 0.35.

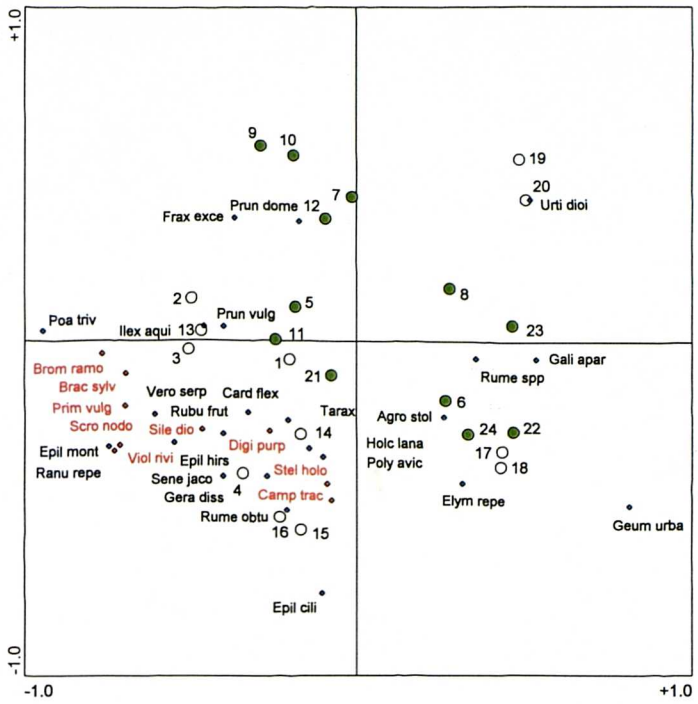


Figure 3.20 Species and sample scatter plot of the first two PCA axes from the 1998 Italian alder vegetation data. Samples are colour coded according to light treatment and species according to their origin (see Figure 3.19 for key). $\lambda 1$ = 43.4% of species variance; $\lambda 1 + \lambda 2$ = 57.4% of species variance.

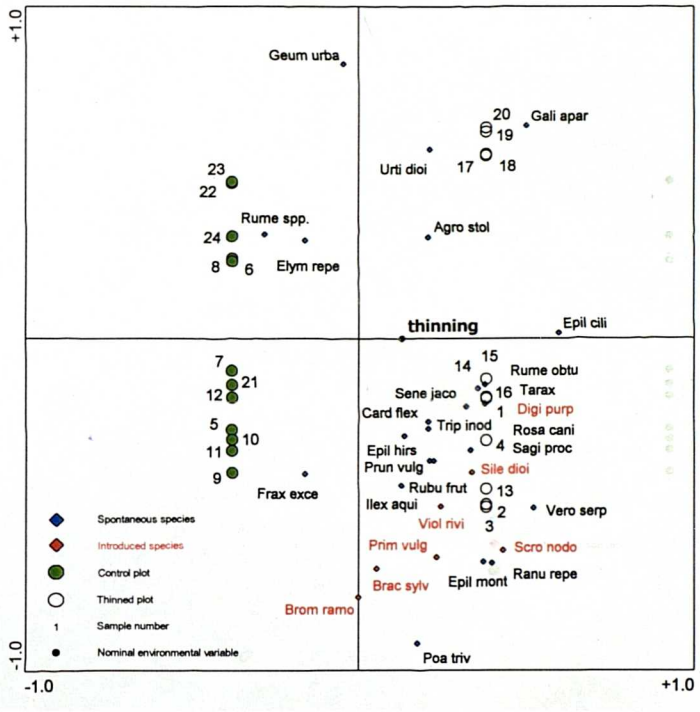


Figure 3.21 RDA Triplot of species, samples and significant environmental variables for the 1998 Italian alder vegetation data. Samples are colour coded according to light treatment and species according to their origin. $\lambda 1$ = 9% of species variance = 100% of species-environment relation. $\lambda 1 + \lambda 2$ = 51.3% of species variance = 100% of species-environment relation. All axes are significant and the sum of all canonical eigenvalues is 0.09.

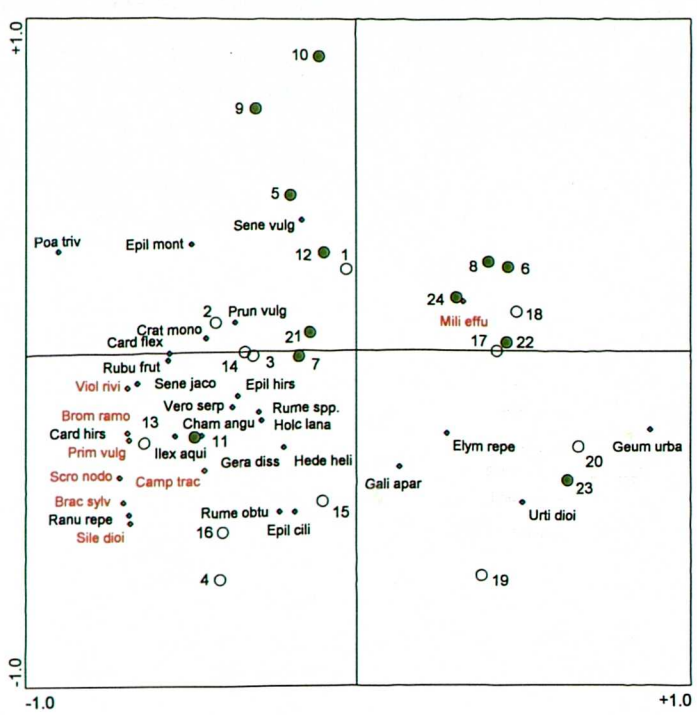


Figure 3.22 Species and sample scatter plot of the first two PCA axes from the 1999 Italian alder vegetation data. Samples are colour coded according to light treatment and species according to their origin (see Figure 3.21 for key). $\lambda 1$ = 47.3% of species variance; $\lambda 1 + \lambda 2$ = 58.8% of species variance.

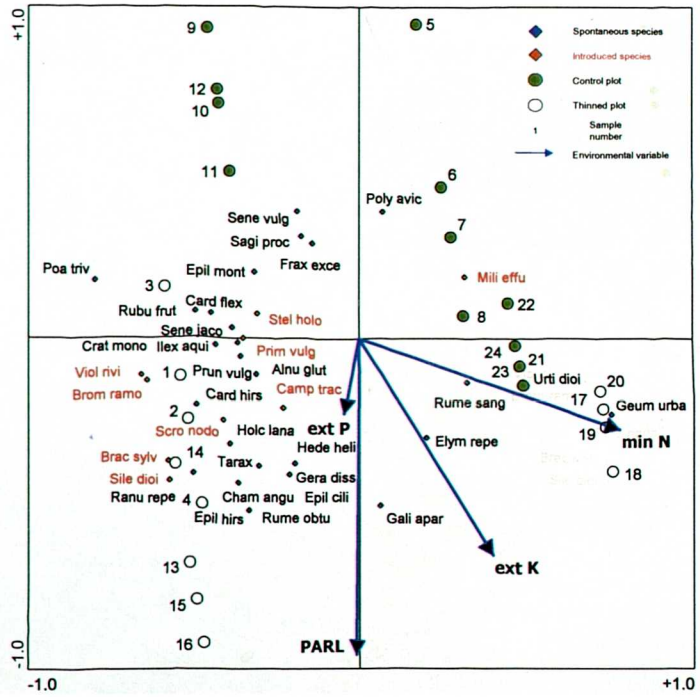


Figure 3.23 RDA Triplot of species, samples and significant environmental variables for the 1999 Italian alder vegetation data. Samples are colour coded according to light treatment and species according to their origin.
$\lambda 1$ = 33.5% of species variance = 71.1% of species-environment relation.
$\lambda 1 + \lambda 2$ = 40.7% of species variance = 86.5% of species-environment relation.
All axes are significant and the sum of all canonical eigenvalues is 0.471.

Figure 3.24 Mean densities of introduced species occurring in 1998 in thinned and unthinned plots in the Norway maple plantation of Experiment 1. Letters denote statistical difference between means ($p < 0.05$).

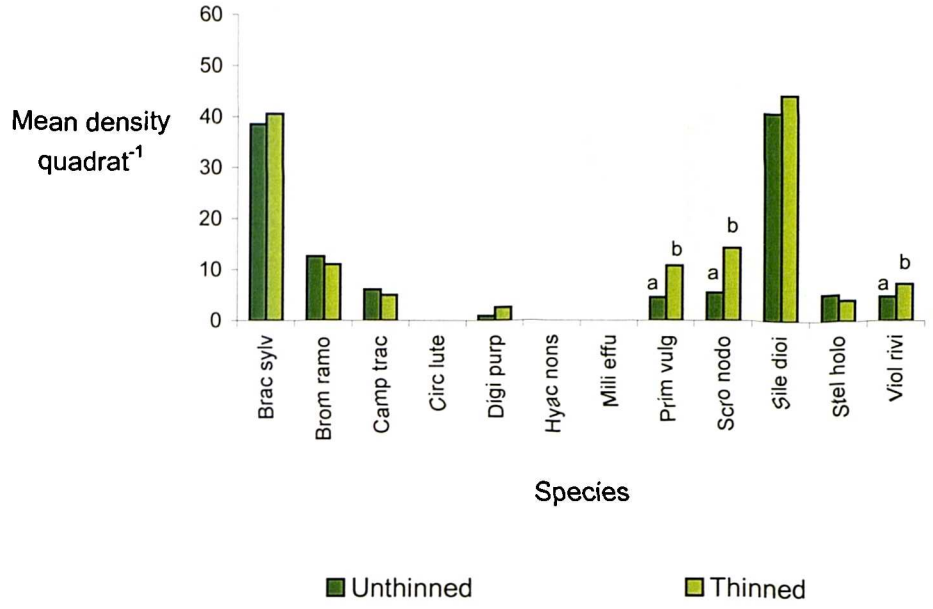


Figure 3.25 Mean densities of introduced species occurring in 1999 in thinned and unthinned plots in the Norway maple plantation of Experiment 1.

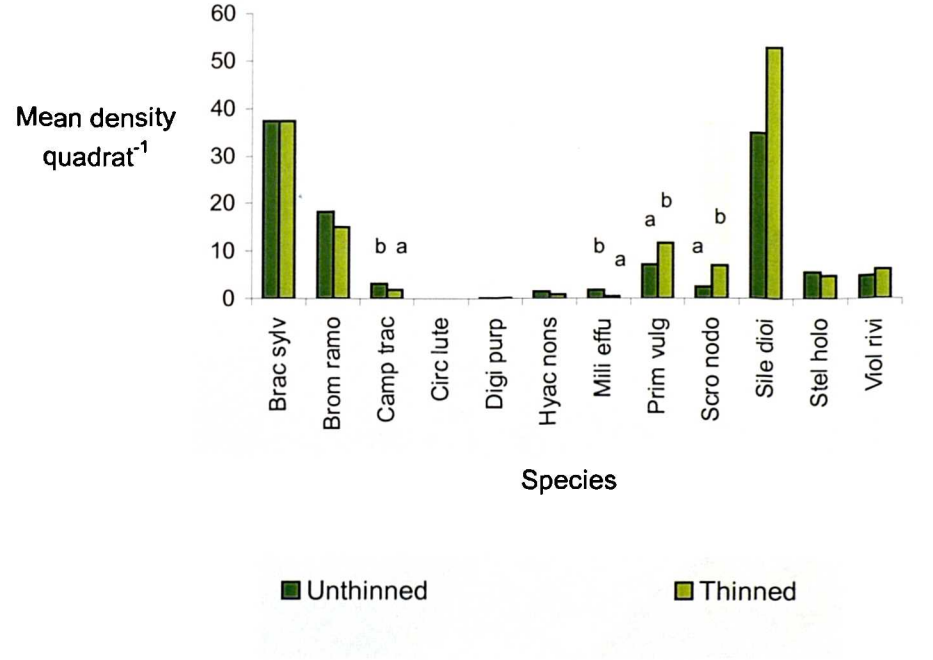


Figure 3.26 Mean densities of introduced species occurring in 1998 in thinned and unthinned plots in the Italian alder plantation of Experiment 1. Letters denote statistical difference between means ($p < 0.05$).

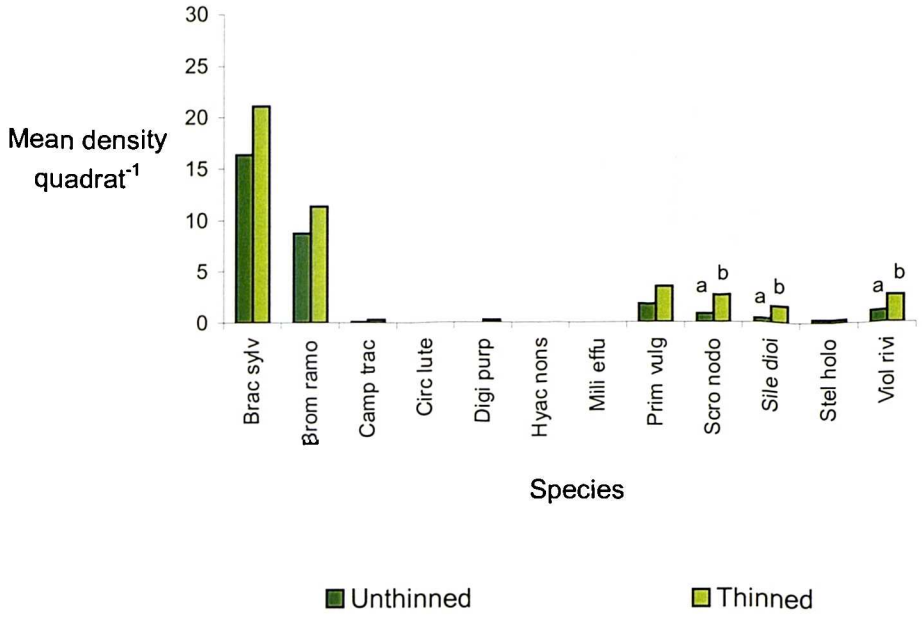
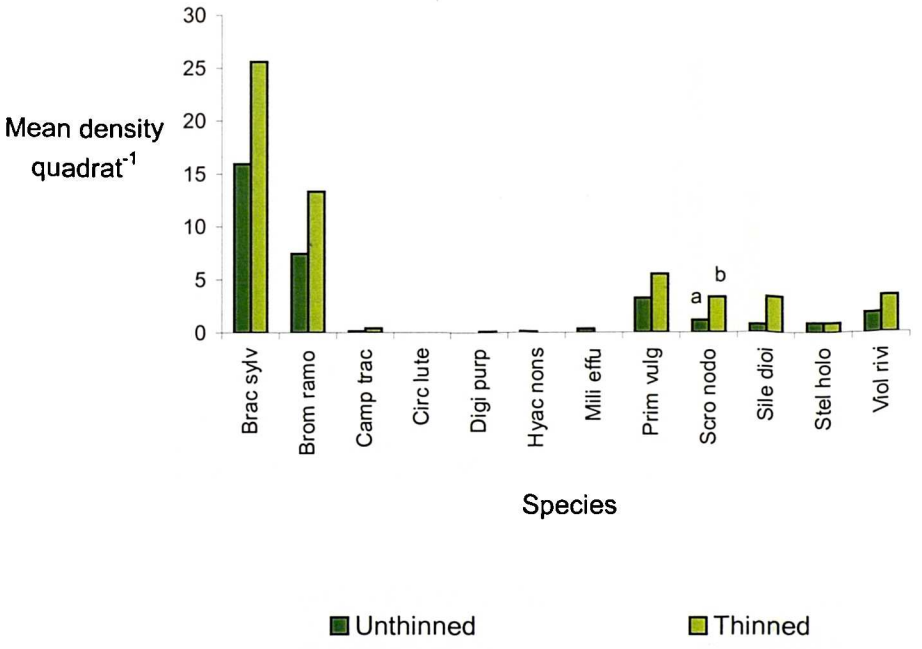


Figure 3.27 Mean densities of introduced species occurring in 1999 in thinned and unthinned plots in the Italian alder plantation of Experiment 1.



Chapter 4: Soil Fertility and Light Manipulation Experiments: Experiment 2: A Field Experiment at Nedge Hill

4.1 Introduction

Experiment 2 (Section 2.1), at Nedge Hill, Telford (Section 2.2.2), was designed to complement the results of Experiment 1 (Chapter 3), the Light Manipulation Field Experiment as well as Experiment 3, the Soil Fertility and Light Manipulation Experiment in experimental ground flora communities (Chapter 5). Experiment 2 was established to investigate environmental influences on the development of enhanced ground flora communities within a mixed plantation. Experiment 2 had a larger experimental area and treatment plots than Experiment 1, with a 'whole wood' buffer zone and was designed to minimise treatment plot and plantation edge effects, which influenced results in Experiment 1. The mixed canopy at Nedge Hill more closely resembles an ancient semi-natural broadleaved woodland than the monospecific plantations used in Experiment 1 (Section 2.2). In Experiment 2, both the light climate and soil fertility were manipulated in replicated plots. The ground flora response to soil fertility and light intensity were measured at the community and species level.

4.1.1 Aims and objectives

The central aims of Experiment 2: The Soil fertility and Light Manipulation Experiment at Nedge Hill were to:

- Test the hypothesis that in combination and in interaction, soil fertility and light intensity are major determinants of vegetation development in enhanced ground flora communities.

- Define ranges of soil fertility and light intensity which optimise vegetation development in the direction of target communities (Section 1.4.5).

The objective of Experiment 2 was to investigate field layer plant communities that develop following species introductions in established plantation woodland, in relation to variations in light regime (manipulated by selective canopy thinning) and soil fertility (manipulated by addition of compound agricultural fertiliser).

4.2 Methods

4.2.1 Establishment

An experimental area of 1440 m^2 (72 x 20 m) was marked out within a *c.* 30 year old, mixed mostly broad-leaved plantation, on former agricultural land at Nedge Hill, Telford (see Section 2.2.2 for site description). The experimental area was selectively thinned on 30/01/98 providing two light treatments, 100% and 50% of the previously existing canopy cover, each replicated three times. The experimental area was surrounded by a 'whole wood' buffer zone. The long axis of the experiment ran 72 m down-slope in a north-westerly direction and parallel to a narrow grassy ride. A 5 m buffer zone screened the experiment from ride side light. Beyond this buffer strip, the experimental area ran 20 m slightly down-slope into the wood, in a south-westerly direction. The north-westerly slope was the main slope in the experiment, hence the design to minimise slope effects. Treatments were laid out in series perpendicular to the ride. Each light treatment measured 12 m x 20 m. Two fertility treatments were superimposed on to the light treatments in a factorial design. Figure 4.1 shows the relative location and experimental layout of the treatment plots and sample positions.

The tree canopy within the experimental area was dominated by *Fraxinus excelsior* at a mean abundance of 50% cover. Although *Fraxinus* dominated the canopy across the experiment, it's cover was reduced down-slope along the long axis of the experiment, with mean percentage cover of 60%, 50% and 40% in blocks 1, 2 and 3, respectively (Figure 4.1). *Quercus robur* and *Prunus* spp. (ornamental cherry) were fairly evenly distributed throughout the canopy (~ 10% mean cover). *Acer platanoides* occurred occasionally as a canopy tree, throughout the area, but occurred at higher abundances in blocks 2 and 3 (10% mean cover), compared to 5% in block 1. *Acer campestre* and *Sorbus aucuparia* occurred as minor canopy components (accounting for < 5% mean cover) in blocks 2 and 3 and in block 3, respectively. *Fagus sylvatica, Aesculus hippocastanum* and *Castanea sativa* were canopy occasionals, with < 10% mean cover in blocks 2 and 3.

The shrub layer was dominated by *Crataegus monogyna,* which occurred throughout the experimental area (20% mean cover). The distribution of *Crataegus* mirrored that of *Fraxinus* in the canopy, with 34%, 17% and 12% mean cover in blocks 1, 2 and 3, respectively. Most of the canopy species were present at low levels (< 5% cover) in the shrub layer, with the exception of *Quercus robur* and *Fagus sylvatica. Sambucus nigra*

occurred occasionally at < 2% mean cover in blocks 1 and 2. The distribution of tree species in the shrub layer largely reflected their distribution in the canopy. The exception to this was *Fraxinus* (< 5% mean cover), which was absent from block 1, where its canopy component was most abundant.

The entire experimental area was sown with the standard seed mix (see Table 2.1 for seed mix details and Section 2.3 for application methods) on 14/02/98 and 15/02/98. Plates 4.1 and 4.2 illustrate the experiment at establishment in control and thinned plots, respectively. The factorial design onto which fertility treatments were established can clearly be seen. The sparse and patchy background vegetation is described in Section 4.3.1. The fertility treatments comprised a top dressing of N:P:K compound agricultural fertiliser at a standard field rate of 100 kg ha^{-1} (fertilised) and a control (unfertilised). The fertiliser was applied by hand in two even doses, administered three weeks apart, on 03/06/98 and 24/06/98, to minimise scorching (Section 2.1.2).

4.2.2 Light monitoring

Light monitoring was carried out during the woodland dark and light phases, of summer 1999 (08-10/09/99) and winter 1999/2000 (24/02/00 and 29/02/00), respectively. PAR was measured as described in Section 2.4. Mean sample PAR measurements were expressed as a percentage of the mean ambient solar radiation reaching open ground adjacent to the plantation. The percentage tree canopy cover above each quadrat was recorded at the time of the vegetation survey.

4.2.3 Vegetation survey

The field layer vegetation was surveyed during the spring / summer of both 1998 and 1999, as described in Section 2.5 (i.e. between 06/08/98-21/08/98, and 12/05/99-26/05/99). The late survey dates during the first growing season reflect the protracted establishment of the experimental programme. Quadrats were positioned as shown in Figure 4.1.

4.2.4 Soil survey and analysis

On 27/05/99, soil sampling was undertaken (Section 2.6.1). Due to the time and resource limitations of the experimental programme, a soil sampling strategy was devised for Experiment 2 which gave a broad indication of soil fertility across the entire experiment as well as providing more detailed insight into within plot variation. This was achieved

by: a) taking a topsoil sample from the centre of each quadrat; these samples were then bulked to form a single composite sample for each fertility treatment replicate; and b) taking five topsoil samples from each quadrat (from the centre and four corners), within the first light treatment replicate (plots 1 and 2 in Figure 4.1) and bulking these to form a single sample for each quadrat. The first light treatment replicate was chosen for detailed soil analyses, because it had produced the most marked vegetation response. Soil samples were prepared and stored as described in Section 2.6.1. Chemical analyses were carried out to quantify indicators of soil fertility. Soil pH and mineralisable nitrogen, extractable phosphorus and potassium, plus percentage soil organic matter were measured, as described in Sections 2.6.2-2.6.6, respectively.

4.2.5 Statistical analysis and data presentation

4.2.5.1 Environmental variables

4.2.5.1.1 Surfer mapping

Key environmental variables, as well as certain vegetation parameters and response variables, were spatially mapped using kriging as a method of data interpolation, performed in the Surfer 6.01 (Golden Software Inc., 1993-1995) software package (Section 2.7.1.1).

4.2.5.1.2 Parametric analyses

The Genstat 5 Committee (1993) statistical package was used to perform ANOVA on all environmental variables and vegetation parameters. These included the 'vegetation environmental variables' percentage cover of bare ground, bryophytes, litter and woody brash, plus vegetation response measures i.e. the density of introduced species, measured collectively and individually (Section 4.2.5.3). These were measured in both growing seasons to investigate between-block variation and treatment effects (Section 2.7.1.2). The ANOVA were set up using the factorial design as a two-way ANOVA (in randomised blocks). Light treatments were not randomised within blocks, but regularly placed to minimise the main slope effect (Figure 4.1). Treatment significant results are presented in ANOVA tables and tables of treatment means (with the exception of individual species density data, whose treatment means are shown in bar charts (Section 4.2.5.3)). Environmental variables which showed a significant difference between blocks are presented in the same way. Significant interactions between the light and fertility treatments (where both main effects were also significant) are presented as line graphs.

4.2.5.2 Vegetation and environmental data

4.2.5.2.1 Classification: TWINSPAN analyses

All analyses described in this and the following Section (4.2.5.2.2) were carried out on data from the two growing seasons. The multivariate vegetation sample data were classified using TWINSPAN (Hill, 1979a) to aid description of the plant communities which developed following species introductions. Results are displayed in dendrograms. TWINSPAN end group maps were also produced to show the distribution of the main plant 'communities' (Section 2.7.2.1).

4.2.5.2.2 Ordination: CANOCO analyses

Environmental variables representing soil fertility (Section 4.2.4) and the light climate (Section 4.2.2.), plus 'vegetation environmental variables' (Section 3.2.5.1.2), were examined against vegetation response using CANOCO (Section 2.7.2.2), to investigate their potential influences on the establishment of introduced species and on the direction of vegetation development. The environmental variables, measured in both seasons, the thinning and fertilisation treatment variables, percentage canopy cover, percentage cover of bryophytes and percentage of bare ground, litter and woody brash were used in direct gradient analysis of vegetation data from both years. Due to the hypothesised slope effect on vegetation, the x and y co-ordinates of each quadrat centre were used as two further environmental variables in all constrained ordination analyses. As soil variables and PAR measurements were only obtained in the second year of the experiment, these variables were only used in direct gradient analyses of 1999 vegetation data. The above analyses were run separately on the full vegetation data set and on the spontaneous vegetation data set, in the latter case with the introduced species included as environmental variables in RDA. PCA results are presented in scatter plots, some with all environmental variables passively superimposed, to illustrate their relative effects, and RDA results are presented in triplots (Section 2.7.2.2).

4.2.5.3 Species density data

To investigate whether the thinning and fertilisation treatments influenced introduced species density, ANOVA with LSD (Section 2.7.3.2) were performed on quadrat density data (i.e. number of individual plants) summed for both all introduced species and individual introduced species from both growing seasons. Results are presented in ANOVA tables, tables of means and bar charts (Section 4.2.5.1.2). The variation in total introduced species density was also mapped, as described in Section 4.2.5.1.1.

4.3 Results

4.3.1 Physiognomy

The sparse and patchy nature of the background vegetation can just be made out in the establishment photographs (Plates 4.1 and 4.2). This patchy ground flora was characterised by competitive ruderal and woodland species, such as *Urtica dioica, Rubus fruticosus* agg., *Geum urbanum* and, in plots 11 and 12, *Glechoma hederacea*. Outside the patches supporting the vigorous vegetation described above, tree seedlings, especially *Fraxinus excelsior*, and bryophytes, tended to be more common. The patches of vegetation were interspersed with areas of bare ground and litter. The woody litter component, although rarely coarse enough to constitute woody brash, was considerable in places and had probably been increased by the thinning operation.

The patchy nature of the background vegetation is probably largely due to differing canopy characteristics within this mixed plantation. The presence of an intermittent, low growing shrub layer, comprising mostly *Crataegus monogyna* with occasional suckering cherry (Plate 4.1) adds to the architectural complexity of the tree canopy. The presence of a shrub layer within this established mixed-species plantation provides a closer semi-natural woodland analogue than the mono-specific plantations of Experiment 1.

The first season (1998) vegetation response was extremely patchy, but showed marked differences between thinned and unthinned plots. In the thinned plots, the spontaneous vegetation was taller and more vigorous and the introduced species, particularly *Brachypodium sylvaticum*, were more prevalent. Unlike the first season response in Experiment 1, the ground flora in Experiment 2 was not dominated or characterised by introduced species. The first season response was most marked, in terms of the establishment of introduced species, in thinned plots 1 and 2.

The vegetation present in the second year (1999) after establishment is shown in Plates 4.3-4.6. Plate 4.3 shows the low sparse field layer typical of an unthinned plot. This vegetation is characterised by bryophytes and *Fraxinus excelsior* seedlings, with scattered competitive ruderal and woodland species. The introduced species *Brachypodium sylvaticum* and *Hyacinthoides non-scripta* occurred frequently. *Hyacinthoides non-scripta* was not recorded until 1999 and seemed preferentially associated with unthinned plots. With the exception of the introductions, this community

is still similar in appearance to the pre-experiment background vegetation, described above.

Second season vegetation response occurring in the thinned plots is shown in Plates 4.4–4.6. Plate 4.4 shows detail of this vegetation, which although similar to the background vegetation and that in unthinned plots, tended to be denser and more vigorous, with introduced species forming a larger and more consistent component. Plates 4.5 and 4.6 clearly demonstrate the vigorous nature of the vegetation in thinned plots. Here the field layer is a mosaic of tall and short herb forms, characterised by bryophytes, tree seedlings, spontaneous competitive ruderal and woodland species, plus introduced species, such as *Brachypodium sylvaticum, Silene dioica* and *Viola riviniana. Silene dioica* and *Scrophularia nodosa* contribute to the vertical structure of the field layer and along with spontaneous species, such as *Urtica dioica* and *Rubus fruticosus* agg., create a patchy surrogate canopy which overtops small stature herbs, such as *Viola riviniana.*

In summary, the plant communities exhibited a visual response to canopy thinning, although this is less marked than in Experiment 1. A taller denser community was produced in thinned plots. The patchy nature of the vegetation blurred interfaces between treatments. The abrupt treatment boundaries evident in the vegetation response in Experiment 1 were absent in this experiment. No visual response to fertility treatment was discernible.

4.3.2 Environmental variables

4.3.2.1 Light climate

A sunfleck pattern can be seen on the vegetation in Plate 4.6. It was hypothesised in Section 4.3.1 that the patchy nature of the background and introduced vegetation was probably largely due to the differing canopy characteristics within this mixed plantation. The contour maps in Figures 4.2 and 4.3 show the light climate for the 1999 woodland dark and light phases, respectively and these show a spatial correlation between thinning treatment and higher light levels, which is less pronounced during the woodland light phase. The results of ANOVA on the light climate variables (i.e. mean PAR reaching the woodland floor during the woodland dark (PARD) and light phases (PARL), percentage canopy cover recorded in the 1998 (Canopy 98) and 1999 (Canopy 99) woodland dark phases) are shown in the ANOVA table (Table 4.1) and the table of means (Table 4.2). Thinning treatment had a highly significant impact on the light regime, during both

woodland dark and light phases. A higher light climate was evident in thinned plots, regardless of which light climate variable was investigated. PARL and Canopy 99 also showed significant differences between block means (Tables 4.3 and 4.4), indicating that a position effect was influencing elements of the woodland light climate. Block 1 exhibited the lowest dark phase canopy cover and the darkest light phase light regime, suggesting that these light climate variables were not directly related. The response variable PARD showed a significant interaction between light and fertility treatments (Figure 4.30). Figure 4.30 shows that thinned plots have a higher light climate than unthinned plots, but that thinned plots which were also fertilised have a significantly higher light regime than their unfertilised counterparts. CANOCO analyses (Section 4.3.3.3) have been used to further identify which aspects of the woodland light climate had greatest influence on the vegetation.

4.3.2.2 Soil environment

Significant ANOVA results on soils variables are shown in the ANOVA tables (Tables 4.1 and 4.3) and means are presented in Tables 4.2 and 4.4 for treatment significant and block significant variables, respectively. Figures 4.4 and 4.5 show the spatial variation across the experiment in concentrations of soil mineralisable nitrogen and extractable potassium, respectively. Although some association with fertility treatment is apparent from the contour maps, 11 months after fertiliser application, neither light nor fertility treatment significantly affected the distribution of soil nitrogen or potassium (Table 4.1). The effect of fertility treatment was significant on the spatial variation in extractable phosphorus (Table 4.1 and Figure 4.6). Soil phosphorus concentrations were higher in control or unfertilised plots compared to fertilised plots (Table 4.2). This may be due to a fertility reduction effect, whereby fertilisation, and the associated disturbance, allowed increased leaching losses (Persson and Wiren, 1995) or stimulation of plant cation uptake from deep in the the soil profile (Turner and Lambert, 1986). Potassium follows a similar pattern to phosphorus (Figure 4.5), but levels were not significantly different between fertility treatments (Table 4.1). Baseline conditions of soil fertility are unknown, however, the banded patterns in Figures 4.4–4.6 suggest the influence of fertility treatment upon fairly uniform background distributions of mineralisable nitrogen, extractable potassium and phosphorus. Although Figure 4.4 suggests a slight gradient in mineralisable nitrogen acting along the x-axis of the experiment, the lack of significant difference between the block means does not support this (Table 4.3).

Figure 4.7 shows the spatial variation in pH across the experiment. Neither thinning nor fertilisation treatments affected soil pH (Table 4.1). An apparent background pH gradient occurred with levels increasing in a south-easterly direction, along the x-axis of the experiment (Figure 4.7). Higher pH values were associated with the first replicate of the experiment (block 1 in Figure 4.1) (Table 4.4). Variation in the percentage of soil organic matter is shown in Figure 4.8, which was unaffected by light or fertility treatment, and follows a similar pattern to pH, showing significant differences between all block means (Table 4.4).

In summary, the soil in Experiment 2 appeared to exhibit a fairly uniform background fertility, which allowed experimental manipulation of the three main macronutrients. Although only phosphorus was significantly altered by fertility treatment, pH and organic matter gradients existed across the plantation, which probably reflect baseline conditions.

4.3.3 Vegetation and environmental data

4.3.3.1 Vegetation environmental variables

The woodland light climate and soil environment combine with other vegetation parameters (i.e. percentage cover of bare ground, bryophytes, leaf litter and woody brash) and topography to produce a surface microclimate which will influence field layer vegetation. This vegetation, in turn, affects the microclimate and germination niches, crucial to successful ground flora enhancement. The mapping and ANOVA results (Sections 4.2.5.1.1 and 4.2.5.1.2) relating to the total density of the introduced species are presented in this section, as this variable is considered to represent a measure of vegetation response. The results for the individual species density data are considered to represent response at the species rather than community level and are presented in Section 4.3.4.

In the Norway maple plantation of Experiment 1, bryophyte cover was correlated with field layer plant distribution (Section 3.3.3.1). The spatial distribution of the percentage cover of bryophytes, bare ground and litter, in 1999, in Experiment 2 are shown in the contour maps in Figures 4.9, 4.10 and 4.11, respectively. The distribution of bryophytes (Figure 4.9) is broadly inverse to that of bare ground (Figure 4.10). Fertility treatment significantly affected bryophyte distribution in 1998, with higher percentage cover occurring in fertilised plots; however, no such effect was detected in 1999 (Tables 4.1 and 4.2). The percentage cover of bare ground changed from a block effect in 1998

(Table 4.3) to a treatment effect in 1999 (Table 4.1). In 1998 bare ground cover was significantly different in all blocks with block 2 exhibiting the lowest cover (Table 4.4). In the second year after establishment, more bare ground occurred in unthinned plots and fertilised plots (Table 4.2). The major influence on litter cover was a block effect (Figure 4.11, Tables 4.1 and 4.3) with far higher percentages in block 3 in both years (Table 4.4). However, thinning did affect the distribution of litter in the first year (Table 4.1). It was hypothesised in Section 4.3.1 that thinning might have increased litter cover; but the evidence suggests that the operation actually reduced it (Table 4.2). Figure 4.11 suggests that litter increased down-slope in two directions along the length and width of the experimental area. The pattern of litter distribution is mirrored by that of woody brash (Table 4.4), with a gradient increasing down-slope along the x-axis of the experiment (Section 4.2.1). CANOCO analyses using sample position in two dimensions as environmental variables helped elucidate the position effect on litter cover (Section 4.3.3.3).

The effects of the distribution of bare ground and litter on woodland ground flora communities are well documented (e.g. Graae and Heskjaer, 1997; Musgrove, 1998). It is hypothesised that litter may provide a physical barrier that inhibits the germination and establishment of introduced species, and that occurrence of bare ground and bryophytes are likely to favour establishment by providing niche space and ameliorating niche microclimate, respectively. Contour maps of the density distribution of introduced species in the two successive growing seasons are shown in Figures 4.12 and 4.13, respectively. Figure 4.12 shows that introduced species have initially established in two 'hotspots' in plots 1 and 9, which were both thinned and fertilised. This is supported by the statistical evidence, which shows that the density of introduced species is greater in thinned plots and fertilised plots (Tables 4.1 and 4.2).

The patchy, but more widespread distribution of introduced species occurring in the second year (Figure 4.13) is positively associated with the distribution of bare ground (Figure 4.10) and the summer light climate (Figure 4.2). Tables 4.1 and 4.2 show that thinning still exerted a strong positive influence on the total density of introduced species in 1999. However, fertility treatment ceased to have an effect and block effects were as important, with significant differences between all block means (block 2 supporting the lowest densities and block 1 the highest) (Table 4.4). This pattern of block means mirrors that of bare ground at establishment (Table 4.4), which supports the above

hypothesis that the occurrence of niche space in the form of bare ground is conducive to the establishment of introduced species. Bryophyte distribution (Figure 4.9) appears to have no spatial relationship with the density of introduced species (Figures 4.12 and 4.13). The relationship between litter and introduced species density (Figures 4.11 and 4.13) is less clear, with areas of negative and positive coincidence. CANOCO analyses have been used to further investigate the potential influence of cover of bryophytes, bare ground and litter on the vegetation (Section 4.3.3.3).

4.3.3.2 Classification: TWINSPAN analyses

To evaluate the success of the species introductions, TWINSPAN sample classification was used to aid description of plant communities which developed in the first year, and to identify niches and communities into which introduced species have the potential to become established. Analysis of second season vegetation data was used to verify consolidation of niches by introduced species and to track the early development of these enhanced ground flora communities. Bryophyte species have not been included in the reported TWINSPAN analyses, but their percentage cover was examined in Section 4.3.3.3.

TWINSPAN classifications of samples (quadrats) from each of the two years are displayed in dendrograms (Figures 4.14 and 4.15, respectively). Figure 4.14 shows the TWINSPAN classification of the 1998 vegetation data from Experiment 2. Group 0 is a large heterogeneous group, characterised by a high abundance of *Fraxinus excelsior* seedlings and vigorous woodland species, such as *Geum urbanum* and non-woodland ruderals like *Ranunculus repens* and *Taraxacum*. This group comprises 76% of the samples and contains a proportionate number of quadrats from each treatment. This division does not appear to be related to experimental treatment and is perhaps more representative of pre-establishment background variation within the vegetation. Many of the introduced forbs are preferential to Group 0 at low levels of abundance. By contrast, the smaller Group 1 is more homogeneous and is characterised by the presence of *Glechoma hederacea,* plus *Urtica dioica* and *Rubus fruticosus* agg. (a preferential species) at intermediate and high levels of abundance.

Further differentiation of the vegetation at the division of Group 0 separates 19% of samples from Group 0, into Group 00, which are characterised by the presence of the spontaneous species *Geranium robertianum, Epilobium montanum, Holcus lanatus* and

Poa trivialis. The larger Group 00 is defined by a relatively high abundance of *Fraxinus excelsior* seedlings and *Geum urbanum*. Introduced species were not preferential in this division. As with the previous division, all treatments are proportionately represented in each group, indicating that treatment effect is not apparent at this level of division (Figure 4.16). This contrasts with results from Experiment 1, described in Section 3.3.3.1, and perhaps indicates the difficulties of imposing experimental treatments on to an established and complex woodland system.

As treatment effect is not apparent in the previous divisions and the impact of the introduced species on the vegetation is minimal, Group 01 is further divided into Groups 010 and 011, comprising 59% and 41% of Group 01 samples, respectively (Figure 4.14). Group 010 is characterised by the presence of *Geum urbanum* and *Rubus fruticosus* agg. at high levels of abundance, plus a high proportion of samples from control plots (Figure 4.16). Group 011 represents a weedy woodland community indicated by abundant *Urtica dioica* and low levels of *Galium aparine, Ranunculus repens, Epilobium montanum* and *Hedera helix*. This suite of species could indicate an established woodland community that has undergone disturbance or enrichment, perhaps caused by the experimental treatments. Group 011 contains a disproportionate number of samples from treated plots, both thinned and fertilised, including those which were subject to both treatments (Figure 4.16). This group also contains a high proportion of quadrats from plots 1 and 2 (Figure 4.16), which appeared to have produced the most successful establishment of introductions, on visual observation alone (Section 4.3.1). However, introduced species are not preferential to the group.

Group 1 on the positive side of the dendrogram (Figure 4.14) is divided into two fairly even sized Groups 10 and 11. Samples from the two fertility treatments are proportionately assigned to the groups at this division (Figure 4.16). Group 10 contains 89% of the available thinned samples, i.e. those from Group 1 (Figure 4.16). Group 11 is largely composed of samples from the lower half of plots 11 and 12, and has a disproportionate number of samples from control plots (Figure 4.16). Thinning significantly increased irradiance reaching the woodland floor during summer (Section 4.3.2.1) and a light treatment effect is evident at this division. Group 10 is characterised by *Galium aparine* (1), the introduced grass *Brachypodium sylvaticum* and high abundance of *Urtica dioica*. The presence of the annual indicator species *Galium*

aparine perhaps suggests disturbance due to thinning. Group 11 is characterised by the presence of *Glechoma hederacea* and *Heracleum sphondylium.*

To summarise, the 1998 vegetation was a patchy weedy woodland community whose heterogeneity appeared to be more related to background environmental variations than experimental treatment. The introduced species had little overall impact on this vegetation in the first season after establishment. There is some evidence to suggest that the increased light levels and disturbance caused by thinning favoured the establishment of introduced herbs.

The second season (1999) sample classification of vegetation data from Experiment 2 is shown in Figure 4.15. On comparison of the dendrograms in Figures 4.14 and 4.15, the most obvious difference is the increased importance of the introduced species in the second year by way of their appearance as indicator species at every TWINSPAN division. At the first division 73% of samples are split into Group 0, which is characterised exclusively by an abundance of *Urtica dioica.* The positive Group 1 is characterised by woodland and relatively light-demanding woodland edge species, such as *Anthriscus sylvestris* and the introduction *Silene dioica.* Although the sample allocations were similar at the first division in the two growing seasons (Figures 4.14 and 4.15), the groups are indicated by different species. *Urtica dioica* (3) characterises the negative Group 0 in 1999 (Figure 4.15), whereas in 1998 this species at psuedospecies level 2, along with *Glechoma hederacea* (1), is indicative of Group 1. This may indicate the increasing importance of *Urtica* in providing a surrogate canopy that influences the establishment of introduced species. The thinning and fertilisation treatments may have encouraged the spread of *Urtica.* As with the 1998 classification (Figure 4.14), the initial division of samples does not appear to be related to experimental treatment.

The division of Group 0 separates 34% of the samples into Group 00, which are characterised by the presence of introduced species *Circaea lutetiana* and *Silene dioica* and an abundance of *Glechoma hederacea.* The larger Group 01 is indicated by abundant *Urtica dioica* and *Poa trivialis,* with *Galium aparine* plus the introduced species *Stellaria holostea* and *Brachypodium sylvaticum.* There is a disproportionate allocation of 81% of thinned samples and 74% of fertilised samples to Group 01. This may indicate that the disturbance and enrichment created by the experimental treatments favour the

establishment of certain introduced species, possibly due to the encouragement of a surrogate canopy, as hypothesised above.

Group 01 is further divided into Group 010 containing 33% of Group 1 samples, and characterised by the introduced grasses *Brachypodium sylvaticum* (2) and *Bromopsis ramosa* (1), plus *Hyacinthoides non-scripta*; and Group 011 with abundant *Urtica dioica* and *Poa trivialis*. At this division, samples are assigned proportionately according to treatment. This division appears to be more related to plot position than treatment influence (Figure 4.17). Plot position effects are investigated below using TWINSPAN end group maps (Figures 4.16 and 4.17).

Group 1 on the positive side of the dendrogram (Figure 4.15) is divided into two fairly even sized Groups 10 and 11. The smaller Group 11 has proportionally more samples from thinned (56%) and fertilised (50%) plots (Figure 4.17), and is characterised by the introduced species *Hyacinthoides non-scripta* and *Stellaria holostea* (Figure 4.15). The presence of *Geranium robertianum* at all abundance levels is most diagnostic of Group 11. This could be interpreted as *Hyacinthoides non-scripta* and *Stellaria holostea* colonising niches within a community dominated by *Geranium robertianum.*

In summary, the 1999 vegetation was still a patchy weedy woodland community whose heterogeneity apparently depended more on background environmental variations than experimental treatment. However, treatment effects, most probably due to thinning, are evident at the second division. Introduced species were clearly an important element of the 1999 vegetation in all but one of the TWINSPAN end groups, perhaps representing wider niche consolidation in the second year (Figures 4.14 and 4.15). It is hypothesised that treatment effects are more protracted and perhaps longer lasting in more established secondary woodlands. There is evidence to suggest that the increased irradiance caused by thinning, and possibly enrichment from fertilisation, favours the establishment and niche consolidation of introduced species. There may be indirect treatment benefits for introduced species, via the encouragement of a tall herb surrogate canopy.

The patchy nature of the vegetation in Experiment 2 recorded during the two respective growing seasons is shown in the TWINSPAN end group maps, which illustrate that sample position is more important than treatment in determining plant communities (Figures 4.16 and 4.17). In 1998, Group 011 is positively associated with thinned and

fertilised plots and Group 11 with unthinned plots (Figure 4.16). In 1999, Group 010 is preferentially associated with thinned plots, Group 00 with control plots and Group 11 with thinned and fertilised plots (Figure 4.17). This evidence suggests that both thinning and fertilisation may benefit the success of introduced herbs, but that their influence is likely to be secondary to other environmental variables acting on the vegetation.

The classification evidence presented in Figures 4.14-4.17 shows that neither treatment is associated with the principal variation in the vegetation and that introduced species may colonise more than one community patch type. Therefore communities positively associated with introduced species fall on both sides of the 1999 dendrogram (Figure 4.15). This indicates that classification, while useful to aid community description, is less useful for elucidating environmental trends within the data which influence plant distribution and hence the nature of the vegetation. The TWINSPAN analyses allow consideration of only the nominal treatment variables and not the continuously varying environmental variables which they affect. CANOCO analyses (Section 4.3.3.3) are more useful at identifying and interpreting continuous gradients within multivariate data sets. TWINSPAN analyses were performed on whole vegetation data sets, whereas CANOCO analyses were used to investigate the spontaneous vegetation (as well as the total vegetation) and the potential relationships with the introduced species by treating them as environmental variables (Section 4.3.3.3).

4.3.3.3 Ordination: CANOCO analyses

The ordination diagrams (Figures 4.18–4.25) were created and presented as described in Section 2.7.2.2. The scatter plot in Figure 4.18 shows the relative positions of both species and samples under a PCA analysis performed on the 1998 vegetation data. ANOVA of the sample ordination scores for the first two axes of variation produced by the PCA reveals no treatment effect on either axis (Table 4.3). However, a highly significant block effect is evident on Axis 2 scores, with block 3 showing the lowest score and block 2 the highest (Table 4.4). This contrasts with results from Experiment 1, where a thinning effect was identified in both plantations (Section 3.3.3.2). This, coupled with the classification evidence (Section 4.3.3.2) and the lack of sample grouping according to treatment along either of the first two PCA axes (Figure 4.18), indicates that neither light nor fertility treatments are major determinants of initial field layer development in Experiment 2. As the thinning treatment affected the summer woodland light climate in both seasons (Section 4.3.2.1) and the fertility treatment influenced

available soil phosphorus in the second year (Section 4.3.2.2), it seems reasonable to conclude that neither light intensity nor soil fertility were the main determinants of early ground flora development in Experiment 2. The strongest treatment pattern in Figure 4.18 is the high proportion of samples from plots which have been thinned and fertilised in the top left and bottom right quadrants of the scatter plot. These samples are perhaps grouped narrowly on an unidentified axis bisecting the top right and bottom left quadrants at about 45°. The introduced species would be at one end of this axis, which could represent an interaction between light and fertility or, an environmental variable independent of light or soil fertility. RDA, described below (Figure 4.20), is used to identify those environmental variables that most influence the vegetation.

The introduced species are tightly grouped in the top right hand quadrant of the scatter plot (Figure 4.18), along with most spontaneous species, including the more light-demanding woodland edge and non-woodland species, such as *Stachys sylvatica* and *Stellaria media*, respectively. This grouping of species by PCA (Figure 4.18) is associated with a relatively small number of samples that come proportionately from all four experimental treatments. This suggests that introduced species have, during the first season, successfully occupied limited and patchy niche space, in a manner that is not influenced by experimental treatment. Of note are the unrelated positions of *Urtica dioica* and *Rubus fruticosus* agg. *Urtica* is preferentially associated with species that might indicate disturbance or enrichment, such as *Galium aparine* and thinned plots. *Rubus* is associated with the more shade-tolerant tree seedlings, such as *Fraxinus excelsior* and control plots.

Figure 4.19 shows the same PCA results as Figure 4.18, but with all environmental variables passively superimposed onto the species scatter plot. The position of the nominal treatment environmental variables at the origin of the scatter plot illustrates that thinning and fertilisation had little influence on the two most important axes of variation in the vegetation data, and supports the classification evidence (Section 4.3.3.2). This is supported by the position of the canopy cover variable (shown in Section 4.3.2.1 to be a good negative analogue for summer light climate), which is not strongly associated with either axis. However, canopy cover shows a clear negative association with the introduced species. Bare ground and litter cover appear closely related, as expected, but unusually, are acting in the same direction, and both negatively associated with introduced species. The influence of bryophyte cover appears to vary in importance for

the different introduced species. The x and y co-ordinates are strongly associated with axis 2 and support the classification evidence (Section 4.3.3.2), in suggesting that position effects, probably related to slope, have a major influence on vegetation establishment. Litter and bare ground are also closely associated with axis 2, suggesting that, along with position (which could be part of the same effect) they are the major determinants of initial ground flora development. Axis 1 has no clear interpretation in relation to the measured environmental variables. RDA was used to determine which of these potential environmental influences was correlated with the vegetation.

The RDA triplot of species, samples and environmental variables in Figure 4.20, shows the environmental parameters that were significantly related to vegetation establishment in 1998. The most notable pattern in the sample ordination is the almost complete separation of thinned and unthinned samples along axis 2 (Figure 4.20). The position of the thinning treatment centroid shows that thinning did have a positive influence on sample distribution along axis 2. Introduced species are positively associated with thinned plots, but to a lesser degree with thinned and fertilised plots, which seem more allied with aggressive woodland species, such as *Rubus fruticosus* agg. and light-demanding non-woodland species, such as *Heracleum sphondylium* and *Holcus lanatus*.

Litter and bare ground were significantly correlated with the vegetation. The vector position of these two variables in Figure 4.20 suggests that they are acting together and could be interdependent, or co-linear. Litter and bare ground are most closely associated with axis 1 and negatively with the y co-ordinates, which is supported by the distribution patterns of these variables (Figures 4.11 and 4.10, respectively). The x co-ordinates (i.e. the main slope in the experiment) appear along with bryophyte cover to be allied with axis 2 and positively associated with the introduced species, with the possible exception of *Silene dioica*. Introduced species are positively associated with plots occurring towards the top of the main slope, as indicated by the x co-ordinates (Figure 4.20). This evidence suggests that less litter cover may favour the establishment of introduced species, i.e. litter can be used as a measure of niche availability. The ANOVA results (Section 4.3.3.1) showed that the distribution of litter cover was mainly influenced by block position (possibly due to a slope effect), but there was a negative correlation with light treatment (Tables 4.1 and 4.2) in the first year. Therefore, although the distribution of litter across Experiment 2 is a background environmental variable, it was initially reduced by thinning (as tree removal reduces the source of litter and opens up the canopy

to increased wind speeds which could disperse litter), creating and ameliorating niche space in thinned plots. This is supported by the negative relationship under RDA between litter and the thinning treatment variable (Figure 4.20).

Introduced species are not necessarily favoured by the presence of bare ground; they are in fact negatively associated with it (Figure 4.20). This is probably because some form of ground cover is likely to ameliorate the niche microclimate, especially with respect to moisture, making it more suitable for germination. Results from the Norway maple plantation of Experiment 1 (Section 3.3.3.3.1) showed how important bryophyte cover can be in this respect. In Experiment 2, bryophytes also appear to have a positive influence on the establishment of most introduced species (Figure 4.20). However, bryophyte cover is most closely associated with thinned and fertilised plots, non-woodland weedy species (Figure 4.20) and edge effects (Figure 4.9).

The RDA triplot of species, samples and environmental variables in Figure 4.21, shows the environmental parameters that were significantly related to the spontaneous vegetation in 1998. Introduced species were tested for significance, as explanatory variables, under manual selection together with all of the measured and treatment environmental variables. As for the entire vegetation data set (Figure 4.20), the main influences on the spontaneous vegetation were litter and bare ground acting in the opposite direction to distance along the y-axis of the experiment. Most species were negatively associated with litter and bare ground. As in Figure 4.20, thinning treatment was positively associated with most species, as was the distance along the x, or long axis, of the experiment. The major difference between the RDAs on the entire and spontaneous vegetation data sets (Figures 4.20 and 4.21) is the lack of thinning influence on the second ordination axis. The introduced species *Brachypodium sylvaticum* and *Silene dioica* are related to the distribution of the spontaneous vegetation, being positively associated with most of the spontaneous species except the grasses, *Glechoma hederacea, Hedera helix* and *Urtica dioica*. The association of *Brachypodium sylvaticum* and *Silene dioica* with most spontaneous species illustrates the broad niche space into which introduced species are becoming established. The *Brachypodium sylvaticum* and *Silene dioica* environmental variables act in a similar plane to the thinning and x co-ordinate variables, and are associated with both fertilised and thinned plots, but not control plots. The evidence in Figure 4.21 suggests that species introductions into established secondary woodland can have a significant impact on spontaneous vegetation

in the first year, and that the success of these introduced species is likely to be enhanced by thinning.

The PCA performed on the 1999 vegetation data in Experiment 2 is shown in Figure 4.22. As in the first year, experimental treatment had no effect on sample ordination scores on the first two axes of variation produced by the PCA, and significant block effects were also detected (Table 4.3). In 1999, the same block score pattern shown on axis 2 in 1998 was evident on both axes 1 and 2 scores, with block 3 exhibiting the lowest score and block 2 the highest (Table 4.4). In 1999, axis 1 PCA scores showed a stronger relationship with block position than axis 2 (Table 4.3). This evidence, from both growing seasons (Tables 4.3 and 4.4), shows the increasing importance of block position, which may, partly, reflect diminishing treatment effects. Direct gradient analyses, discussed later, aided interpretation of the environmental variables responsible for the block effects on plant distribution.

By comparing the PCA results from the two seasons (Figures 4.18 and 4.22) it appears that sample distribution according to treatment is similar, although there is less sample spread along either axis in the second year, perhaps indicating a more stable vegetation. Axis 1 in Figure 4.18 appears to be transposed in species terms in Figure 4.22. However, the treatment plot distribution remains similar, with a disproportionate allocation of samples from thinned and fertilised plots in the top left and bottom right quadrants. As in 1998 (Figure 4.18), introduced species are associated with many of the more light-demanding woodland edge and non-woodland spontaneous species (Figure 4.22). The introduced species are less tightly grouped in the second season, perhaps indicating niche consolidation and spread in the second year. In contrast to 1998, introduced species are positively associated with plots that have been both thinned and fertilised. *Hyacinthoides non-scripta* is the exception to this trend. This species was first recorded in the second year and is preferentially associated with unthinned plots and *Rubus fruticosus* agg. *Urtica dioica* lies apart from the introduced species on the extreme positive end of axis 1 and is still associated with species indicative of disturbance or enrichment, such as *Galium aparine* plus thinned and fertilised plots. On axis 2 most species, including most introductions, are separated from most of the samples, perhaps indicating the limited number of samples that introduced species are associated with (i.e. representing colonisation of limited niche space). There is some evidence (Figure 4.22) to indicate that both thinning and fertilisation favoured introduced species in the second year, more

than at establishment in 1998; there is likely to be a time lag between cause and effect when dealing with vegetation response. Direct ordination using RDA was used to investigate this further and will be discussed later.

Figure 4.23 shows all of the environmental variables passively represented on the species scatter plot of the 1999 PCA results for the first two axes of variation. The results are in some ways similar to those in 1998 (Figure 4.19), but in 1999 more information is available about the light climate and soil environment. The measured light variables, PARD and PARL, act in a similar plane to the thinning treatment, and in the opposite direction to the canopy cover. The soil variables are less obviously related, with fertilisation treatment apparently having little impact, extractable phosphorus and potassium acting in broadly similar directions and opposing mineralisable nitrogen. Mineralisable nitrogen is associated with the light variables, possibly indicating that thinning has influenced mineralisable nitrogen by creating a nitrogen source in the form of decaying tree stumps, and by enhancing microbial denitrification by increased irradiance raising soil surface temperatures. However, there was no parametric statistical evidence to support this (Table 4.1); direct gradient analyses was used to attempt to detect a more subtle relationship. Mineralisable nitrogen is allied very closely with the y co-ordinate variable, perhaps indicating a nitrogen gradient across the short axis of the experiment (possibly related to slope effects); unfortunately the soil sampling strategy was not sufficient to detect trends in this direction (Figure 4.4). Mineralisable nitrogen also acts in the opposite direction to the related litter, bare ground and bryophyte cover. It follows that greater ground cover, with e.g. litter, would inhibit mineralisation by preventing irradiance from heating the soil. However, high cover of bare ground is not conducive to mineralisation, perhaps because there is a deficit of source nitrogen, e.g. in the form of litter.

Whereas the light, nitrogen, phosphorus, potassium, litter, bare ground, bryophytes and y co-ordinate variables seem associated with axis 1, soil organic matter, pH and the x co-ordinate variables appear more allied with axis 2 (Figure 4.23). The trends shown in the pH and soil organic matter contour maps (Figures 4.7 and 4.8) are supported by significant block effects on these two variables (Table 4.4). This evidence suggests that the effect due to the position on the x-axis of the experiment is likely to be strongly linked to the distributions of soil organic matter and pH. Most introduced species appear associated with higher light and mineralisable nitrogen levels, apart from *Hyacinthoides*

non-scripta, which is positively associated with litter cover, and to a lesser extent *Circaea lutetiana* and *Campanula trachelium*. These potential relationships were statistically tested using direct gradient analyses.

The RDA triplot of species, samples and environmental variables in Figure 4.24, shows the measured environmental parameters that were associated with trends in the vegetation in the second year (1999). Neither treatment variable was significant in the second year. Litter was still the most important influence on plant distribution, with most species, including the introductions, being negatively associated with litter cover (Figure 4.11). Control plots are most strongly correlated with the litter variable. The x co-ordinate variable was the second most significant variable under manual selection and is associated with axis 2. This variable appears to represent pH, as speculated above, because the pH vector was almost identical in a very similar RDA, which did not use distance variables to constrain the ordination. Axis 2 may, therefore, represent change in pH with slope. Figures 4.7, 4.12, 4.13 show that introduced species were associated with intermediate pH levels. This supports evidence from the Norway maple plantation in Experiment 1 (Section 3.3.3.3.1).

Dark phase PAR was the third most significant variable under manual selection, followed by, and closely associated with, light phase PAR. As thinning treatment significantly affects both these variables (Section 4.3.2.1), which can be used as measures of light treatment effects, it can be concluded that thinning influenced the vegetation in the second year. Neither the nominal treatment variable, nor its percentage canopy cover analogue, were significant in the second year (Figure 4.24). Most introduced species are positively associated with the higher light climate produced by thinning. The effect on light climate is also illustrated by the positive association between most of the thinned and fertilised samples and the two PAR vectors (Figure 4.24). The significance and position of the light phase PAR vector illustrates the vernal nature of most introduced species. Of the introduced species, only *Hyacinthoides non-scripta* is associated with unthinned plots, deeper shade and greater litter cover. This species is adapted to establishment in deep litter, evades high summer shade, and is probably not associated with 'optimum niches' as these are occupied by other introduced species in the first year (as was the case in Experiment 1, Section 3.3.3.3.1). However, as vegetation recording did not take place until August in the first year, when *Hyacinthoides* would not be visible

above ground, it is not possible to state conclusively that germination of this species did not occur until the second year.

Mineralisable nitrogen and the distance along the y-axis of the experiment, were also significant, and appear related (Figure 4.24). Mineralisable nitrogen, like litter, is correlated with the first axis of variation, but acts in the opposite direction, as evident in the unconstrained ordination (Figure 4.23). Species indicative of enrichment are positively associated with mineralisable nitrogen, e.g. *Galium aparine, Urtica dioica* and *Poa trivialis,* as are the introductions *Stellaria holostea, Brachypodium sylvaticum* and *Viola riviniana. Poa trivialis* is an indicator of high fertility (Sinker *et al.,* 1991) and *Stellaria holostea* can take advantage of more than moderate levels of soil fertility (Lawley, 1999). Most species, including most of the introductions, appear associated with moderate nitrogen concentrations. Relationships between soil fertility and individual species were tested using species density data (Section 4.3.4). The mineralisable nitrogen variable does not appear to be particularly associated with any experimental treatment (Figure 4.24), and this is supported by the ANOVA evidence (Section 4.3.2.2). Variations in soil mineralisable nitrogen (Figure 4.4) cannot, therefore, be attributed to either fertilisation or thinning treatment, and can be considered as background variation. As suggested above, a nitrogen gradient across the short axis of the experiment (y co-ordinate) probably related to slope effects, is predicted. However, experimental design has precluded further testing of this assertion. However, the opposing litter variable does show its negative relationship with distance along the y-axis of the experiment (Figure 4.11).

The RDA triplot of species, samples and environmental variables shows the environmental parameters, including introduced species, which were significantly related to the spontaneous vegetation in 1999 (Figure 4.25). The most important environmental variables influencing the spontaneous vegetation are the same as those for the entire vegetation data set (Figure 4.24). Litter opposes mineralisable nitrogen and distance on the y-axis, all of which are associated with the first ordination axis. The x co-ordinates act in a similar way, but are less strongly associated with axis 2. Dark phase PAR, acts in a similar plane, but is more closely associated with mineralisable nitrogen, and light phase PAR ceased to be significant. Of the introduced species variables, *Silene dioica* and *Viola riviniana* are associated with axis 2, and certain thinned and fertilised plots. *Silene* is associated with light-demanding woodland edge and non-woodland species,

such as *Anthriscus sylvestris* and *Cirsium vulgare*, respectively. *Hyacinthoides non-scripta* is, as expected, strongly positively associated with litter cover, and control plots. Adding the introduced species as environmental variables makes for much tighter sample and species ordinations than in Figure 4.24, which serves to indicate the important impact that these introduced species have on the vegetation.

Initial establishment of introduced species is largely dictated by niche availability and the percentage cover of litter can be used as an inverse analogue for this. Positive niche availability is enhanced by greater nitrogen availability, i.e. where litter levels are optimal in providing some degree of niche amelioration, but not high enough to inhibit nitrogen mineralisation. Later niche consolidation and perhaps further spread into new niche space, can be influenced by thinning treatment in an established secondary woodland. Effects of fertility treatment on the vegetation are more difficult to detect and tend to be indirect, and independent of experimental treatment (e.g. the effects of litter on mineralisable nitrogen). Although fertility treatment significantly affected the distribution of extractable phosphorus (Figure 4.6, Tables 4.1 and 4.2), the multivariate analyses failed to detect a direct relationship with the vegetation in 1999. Cohn (1994) believed that environmental conditions at the time of establishment are critical to the success of introduced ground floras in secondary woodlands. This evidence suggests that in well established plantations, like Nedge Hill, it may be more difficult to influence environmental conditions that dictate initial establishment of introductions. Treatment influence may however, have a more subtle and delayed effect on the direction of development of the enhanced vegetation.

4.3.4 Species density data

ANOVA results are shown in Tables 4.1 and 4.3, for treatment significant and block significant variables, respectively. Treatment means, for both respective years, are presented in Figures 4.26-4.29. Figure 4.26 shows mean densities quadrat^{-1} of introduced species occurring in 1998 in thinned and unthinned plots of Experiment 2. Figure 4.26 illustrates the relative success of establishment of the introduced species and the influence of thinning on this response. *Bromopsis ramosa, Circaea lutetiana, Galium odoratum, Milium effusum* and *Scrophularia nodosa* were not recorded in the first year; one *Hyacinthoides non-scripta* seedling was found. Note that *Primula vulgaris* and *Hyacinthoides non-scripta* did not occur at sufficient densities in 1998 to perform ANOVA. All introduced species grew at higher densities in thinned plots, with

Brachypodium sylvaticum, Campanula trachelium, Silene dioica, Stellaria holostea and *Viola riviniana* occurring at significantly greater densities under a thinned canopy (Figure 4.26). *Campanula trachelium* and *Primula vulgaris* germinated only in thinned plots in the first season. *Brachypodium sylvaticum* was the most successful of the introduced species in the first year, both in terms of niche space colonisation (Figure 4.14) and consolidation, as measured by density (Figure 4.26).

Figure 4.27 shows the effect of fertility treatment on mean densities of introduced species occurring in 1998 in Experiment 2 and illustrates the influence of fertilisation on the relative success of establishment of the introduced species. All species which germinated in the first year did so at higher densities in fertilised plots. *Brachypodium sylvaticum, Campanula trachelium, Stellaria holostea* and *Viola riviniana* occurred in significantly greater numbers in fertilised plots (Figure 4.27). The ability of *Stellaria holostea* to respond positively to fertilisation in terms of presence, cover abundance (Figure 4.24) and density (Figure 4.27) supports the findings of Lawley (1999). *Primula vulgaris* germinated, at very low density, only in fertilised plots in the first season.

The early development of the introduced vegetation (Figures 4.28 and 4.29) largely mirrors that at establishment (Figures 4.26 and 4.27), in terms of relative species density response. The main differences in the response pattern for the second year (Figures 4.28 and 4.29) is the appearance of those species that were not recorded in 1998. Of these species, which appear to be exhibiting some degree of seed dormancy, *Hyacinthoides non-scripta* made the most significant contribution to the vegetation. *Hyacinthoides non-scripta* was more successful in density terms than *Brachypodium sylvaticum.* Figure 4.28 shows the effect of light treatment on mean densities of introduced species in 1999 and illustrates that most of these species are favoured by canopy thinning, with *Brachypodium sylvaticum, Campanula trachelium, Primula vulgaris, Stellaria holostea* and *Viola riviniana* showing statistically significant relationships. Although certain species, *Circaea lutetiana, Digitalis purpurea* and *Galium odoratum,* appear to grow at higher densities in control plots, there is no statistical evidence to support this trend. *Bromopsis ramosa, Campanula trachelium, Primula vulgaris* and *Scrophularia nodosa* only germinated in thinned plots in the second year. *Bromopsis ramosa, Digitalis purpurea, Milium effusum* and *Scrophularia nodosa* did not occur at sufficient densities, or in sufficient plots, in 1999 to perform ANOVA on the data. Figure 4.29 shows the effect of fertility treatment on mean densities of introduced species in 1999. As at

establishment (Figure 4.27), most introductions in the second year (Figure 4.29) were favoured by fertilisation, though only *Viola riviniana* showed a statistically significant relationship.

Statistically significant interactions between light and fertility treatments on the densities of the introduced species *Campanula trachelium* and *Stellaria holostea,* in 1998, were found (Table 4.1) and are shown graphically in Figure 4.30. Although Figures 4.26 and 4.27 indicate that thinning and fertilisation singly enhance the success of these two species in terms of density, Figure 4.30 suggests, that when interactions are taken into account, that neither factor acting alone significantly influences these response variables. This demonstrates that when the two treatments are combined, they interact to produce a significant and powerful positive influence.

Many introduced species show a significant block effect on their density distributions. *Brachypodium sylvaticum, Campanula trachelium, Silene dioica, Stellaria holostea* and *Viola riviniana* exhibit block and treatment differences (Table 4.1), whereas *Hyacinthoides non-scripta* only responded to block effects (Table 4.3). Block means are reported in Table 4.4. The density distribution of *Brachypodium sylvaticum, Hyacinthoides non-scripta* and *Stellaria holostea* all mirror the block distribution of bare ground at establishment, with block 2 supporting the lowest densities and block 1 the highest (Table 4.4). Blocks effects have less influence than treatment effects on *Brachypodium sylvaticum* in both seasons, but on *Campanula trachelium, Silene dioica* and *Stellaria holostea* block effects become more important in the second year (Table 4.1). Conversely, for *Viola riviniana,* blocks are as influential as treatments in the first year and not significant in the second year. *Campanula trachelium* and *Viola riviniana* in 1998 show similar block distribution patterns, with block 2 supporting the lowest densities and block 3 the highest, which do not correspond directly to the block distributions of other environmental variables. *Silene dioica* in year 2 appears to be positively associated with the distributions of litter and woody brash (Table 4.4).

4.4 Discussion

The objective of Experiment 2 was to investigate the ground flora plant communities that develop following species introductions into established secondary woodland, in relation to variations in light climate and soil conditions. Nedge Hill supported a sparse patchy spontaneous ground flora characterised by competitive ruderal and woodland herbs

(Sections 4.3.1 and 4.3.3.1). The heterogeneous nature of the spontaneous vegetation could have come about largely under the influence of a varied tree canopy. Canopy species affect the light climate by way of their architecture and phenology. Tree species will also influence soil properties, such as pH (e.g. Beniamino *et al.*, 1991; Norden, 1994), and will therefore also indirectly influence soil fertility. The amount and nature of litter production influences topographic / surface microclimatic conditions. The influence of canopy composition on light climate and soil fertility affects baseline vegetation and the extent to which introduced species can infiltrate this vegetation. However, the plantation was chosen partly for its apparent evenly mixed canopy, which was confirmed by tree and shrub species mapping. The experiment was also subject to slope effects in two directions (Section 4.2.1). Slope effects on soil fertility can be profound, especially in sandy free-draining soils, such as at Nedge Hill. Patterns of nutrient leaching and attrition, due to slope, will affect soil pH and nutrient availability patterns. Slope is likely to affect macronutrient distribution, causing down-slope leaching, as well as down-slope accumulation of organic matter, which may augment the organic nitrogen and phosphorus pools.

The heterogeneous background vegetation will provide heterogeneous niche space for colonisation, which is made increasingly heterogeneous by experimental treatment, causing a heterogeneous response, which is desirable in terms of resemblance to ancient semi-natural woodland communities. In order to model the heterogeneous response of the introduced species, ordination analyses were used to identify environmental variables that most influenced the vegetation. The environmental variables responsible for the heterogeneous spontaneous vegetation and their effect on introductions were investigated, as well as treatment influences on these variables and the vegetation.

Both classification (Section 4.3.3.2) and ordination (Section 4.3.3.3) evidence shows that thinning treatment significantly influenced the establishment (1998 data) and early development (1999 data) of the enhanced ground flora communities. As thinning treatment affected the light climate, in both years, and both dark and light phase light climate in the second year (Section 4.3.2.1), it can be concluded that light intensity directly influenced the vegetation. However, fertility treatment, which influenced available phosphorus (Section 4.3.2.2), did not have a detectable effect on vegetation. Although fertility treatment was not significant at the community level, it enhanced success of introductions at the species level (Figures 4.27 and 4.29). Certain aspects of

background soil fertility were significantly correlated with the vegetation, both entire and spontaneous, in the second year (Figures 4.24 and 4.25). Light intensity, as affected by thinning treatment, was a major determinant of field layer establishment, but its influence was very much secondary to that of niche availability, as represented by litter (Sections 4.3.3.2 and 4.3.3.3). However, litter distribution is partly dependent on canopy cover and may in fact represent variation in the light climate.

The existence of an established background vegetation dilutes treatment effects on the resulting enhanced communities. This, coupled with a limited window of treatment influence, may create problems, for which relevant management options are discussed in Chapter 6. However, the light climate and soil conditions may be close to optimum for ground flora introductions, which could explain the minimal treatment effects; this will be further explored in Chapter 6. Since treatment effects appear secondary at the community level, and diluted by existing vegetation, environmental variables which are likely to have shaped the pre-establishment vegetation were investigated.

Litter was found to be the single most important variable associated with variations in plant distribution in both seasons (Figures 4.20 and 4.24). This was true for both the entire (Figures 4.20 and 4.24) and spontaneous vegetation data sets (Figures 4.21 and 4.25). In Experiment 2, percentage litter cover (Figure 4.11) can be used as an inverse analogue for niche availability in the existing vegetation. The heterogeneous niche space created the patchy baseline vegetation, which in turn affects niche availability. New colonists, including introduced species and spontaneous non-woodland and woodland edge herbs, are associated with low litter cover (< 25%). Some litter cover (> 5%) is probably beneficial to the germination and establishment of new colonists by ameliorating a harsh microclimate. Bryophytes provided this function in the Norway maple stand of Experiment 1 (Section 3.3.3.3.1). Litter cover was less under a thinned canopy (Table 4.2). Tree removal reduces future litter production, by removing the litter source, but initially adds felling debris to the litter layer. The disturbance associated with thinning redistributes litter, altering localised surface conditions. Although litter cover was reduced by thinning in the first year (Tables 4.1 and 4.2), the main influence on litter distribution was one of plot position. The difference in block means (Tables 4.3 and 4.4) showed a down-slope increase in litter cover along the x-axis of the experiment, which represents the main north-westerly slope (Section 4.2.1). However, the direct ordination analyses (Section 4.3.3.3) showed that litter distribution was more closely related to

position on the y-axis; the opposing relationship of these two vectors indicating a down-slope increase in cover with the south-westerly secondary slope (Section 4.2.1). Litter cover was closely related to bare ground in the first year (Figures 4.20 and 4.21) and mineralisable nitrogen in the second (Figures 4.24 and 4.25).

Bare ground was also a determinant of the vegetation at establishment (Figure 4.20). The spatial distribution of bare ground (Figure 4.10) appears associated with the density distribution of introduced species in the second year (Figure 4.13), supporting the hypothesis that bare ground provides available niche space and thus favours introductions. However, there was no direct statistical evidence to support this, and the negative influence of experimental treatment on bare ground cover (see below) illustrates that this is not a simple relationship. The block distribution of bare ground in the first year shows that highest percentage cover of bare ground was associated with least litter cover (Tables 4.3 and 4.4). However, this is not a predictable inverse relationship. Bare ground cover in 1999 was negatively affected by both light and fertility treatment and not by block position (Tables 4.1 and 4.2). At the community level (Figures 4.20 and 4.21) bare ground appeared positively associated with litter. However, an RDA (excluding the x, y position variables) showed bare ground and litter apparently acting independently of each other, but were both negatively associated with introduced species. Introduced species were negatively associated with litter and bare ground at the community level (Figure 4.20). The predicted simple and opposing effects of litter and bare ground were not evident in this experiment, the picture being more complex and masked by block / slope effects. The ordination evidence (Section 4.3.3.3) suggests that neither high percentages of litter nor bare ground are conducive to the establishment of introduced species. Established vigorous spontaneous woodland species, like *Geum urbanum* and non-woodland ruderals such as *Heracleum sphondylium* and *Rumex obtusifolius,* are more likely to dominate niches with a high proportion of bare ground. By contrast, introductions need intermediate levels of bare ground, with some degree of niche amelioration, either provided by small amounts of litter or bryophytes (Figure 4.20). Bare ground ceased to be significant in the second year (Figure 4.24), perhaps indicating that available niche space and germination are more important in the first year.

Niche availability was not the only factor affecting species colonisation. The varying autecology of the introduced species coupled with unpredictable sowing probability (i.e. uneven sowing of certain species, due to seed characteristics, e.g. seeds of *Circaea*

lutetiana tended to stick together in clumps within the seed-sand mix), caused different species to colonise different patches within the existing vegetation. For example, *Stellaria holostea* and *Brachypodium sylvaticum* tended to colonise *Urtica dioica* patches, *Circaea lutetiana* and *Siliene dioica* were associated with *Glechoma hederacea* patches, while *Hyacinthoides non-scripta* and *Stellaria holostea* readily invaded niches within *Geranium robertianum* clumps (Figure 4.15). Niche availability was altered by first year colonisation. Certain species that were not recorded until the second year appeared more likely to establish at higher densities in control plots (Figures 4.28 and 4.29). These species included *Circaea lutetiana* and *Hyacinthoides non-scripta* (in terms of fertility treatment only). However, there was no statistical evidence to support this, and the RDA sample and species ordination (Figure 4.24) showed no definite relationships between these species and experimental treatment. Evidence from Experiment 1 (Section 3.3.4) supported the hypothesis that much of the suitable niche space was taken up by introduced species which germinated in the first season, and then proceeded to consolidate their position within the 'optimal niches' in the second year, prohibiting germination of new colonists. However, the picture is more complex at Nedge Hill, with treatment effects being secondary to background variables, such as litter. *Circaea lutetiana* and *Hyacinthoides non-scripta* are tolerant of dense summer shade and *Hyacinthoides* is also able to tolerate deep litter.

The only direct effects of fertility treatment were found at species level, with *Campanula trachelium, Stellaria holostea* and *Viola riviniana* establishing at significantly higher densities in fertilised plots in the first year (Figure 4.27). Although this density effect is only significant for *Viola riviniana* in the second year (Figure 4.29), indicating a reduction in treatment influence, second year vegetation response was clearly affected by certain aspects of soil fertility (Figure 4.24). *Stellaria holostea* and *Viola riviniana,* plus the introduced grass *Brachypodium sylvaticum* and *Urtica dioica,* were positively associated with mineralisable nitrogen, which was found to be the most important aspect of soil fertility in Experiment 2. Spatial variations in the concentration of soil mineralisable nitrogen (Figure 4.4) were not affected by experimental treatment (Tale 4.1) or block position (Table 4.3). However, the association between mineralisable nitrogen and distance along the y-axis of the experiment (Figure 4.24) indicates the presence of a slope-related nitrogen gradient. Although mineralisable nitrogen was not affected directly by either experimental treatment, it appears to act in combination with a higher light climate and low litter cover, to promote development of desirable ground

flora communities (Figure 4.24). The available nitrogen pool, as measured by mineralisable nitrogen, may be influenced by thinning treatment, in that increased irradiance reaching the woodland floor, coupled with disturbance of the litter layer, will raise soil surface temperatures and therefore increase microbial activity and nitrogen mineralisation. There was no direct statistical evidence in Experiment 2 to support this hypothesis, although Figures 4.2, 4.4 and 4.24 show some positive association between dark phase PAR and mineralisable nitrogen. The direct ordination of second year data produced by the RDA (Figure 4.24) shows that mineralisable nitrogen is inversely proportional to litter cover. At lower levels of litter cover, more light heats the soil surface, enhancing nitrogen mineralisation. Litter cover was a major determinant of plant distribution in Experiment 2, influencing the amount of nitrogen available to plants. This litter cover effect on one aspect of soil fertility will be compounded by increased irradiance and disturbance caused by thinning. The opposing litter and mineralisable nitrogen variables, which were both influenced by the south-westerly slope across the experiment, were associated most closely with the first ordination axis (Figure 4.24).

The main north-westerly slope (represented by the x co-ordinate variable), shows association with pH and organic matter gradients (Figures 4.7 and 4.8, Table 4.4) and the second ordination axis. The ordination evidence (Section 4.3.3.3) suggests that the pH element of this background gradient may have more impact on the vegetation. The species association with the x co-ordinate variable (Figures 4.20 and 4.24) can be interpreted as representing pH, with introductions associated with intermediate pH levels and *Digitalis purpurea* and *Silene dioica* associated with more acidic conditions. This supports evidence from the Norway maple plantation in Experiment 1 (Figure 3.17), where introduced species were negatively associated with high pH. There was no direct evidence that fertilisation treatment caused soil acidification (Table 4.1), which might favour the establishment of introduced species.

Extractable phosphorus, often the most diversity-limiting nutrient in grassland systems (e.g. Marrs, 1993), although influenced by fertilisation treatment (Tables 4.1 and 4.2, Figure 4.6), had no apparent impact on vegetation response (Figure 4.24). Soil available phosphorus was apparently decreased by fertilisation treatment. This may be due to a fertility reduction effect, where nutrient addition, especially nitrogen, enhances plant uptake of soil phosphorus. The total density of all introduced species was greater in fertilised plots in the first year (Tables 4.1 and 4.2, Figure 4.12), indicating the increased

vegetation response needed to decrease available phosphorus. However, fertility reduction via fertilisation is a controversial subject and results are inconsistent, especially in terms of residual phosphates (e.g. Marrs, 1993; McCrea *et al.*, 2001a). It seems possible that the soils at Nedge Hill are close to optimum in their fertility, which is perhaps why the phosphorus effect, though interesting, has no apparent relationship with the vegetation. Fertility reduction techniques using fertilisation are perhaps not useful in reducing phosphorus concentrations that are sufficiently high to affect diversity, and high residual soil fertility may still be an obstacle to the establishment of desirable ground flora communities in urban secondary woodlands. These issues are further explored in Chapter 6.

No pre-establishment baseline light data were available for the plantation. However, the plantation was chosen in part due to its even tree canopy, to ensure that the thinning treatments were imposed onto a light climate which was as uniform as possible. It is therefore assumed that the pre-establishment light climate was analogous to that of control plots. PAR was not measured at the time of sowing, or during the 1998 growing season, when percentage canopy cover was used as an inverse analogue for light infiltration. The highly significant effect of thinning on all measured light climate variables in both seasons (Tables 4.1 and 4.2) shows that percentage canopy cover is a reasonable inverse analogue for infiltration. The position and significance of the thinning treatment variable and the association of thinned plots with the upper half of axis 1 in Figure 4.20 illustrates the effect of thinning on vegetation establishment. Both dark and light phase PAR were significantly associated with vegetation response in the second year (Figure 4.24). These two temporal aspects of the woodland light climate are interrelated, as a change in one will lead to a proportional change in the other; e.g. tree removal via thinning allowing higher levels of irradiance to reach the woodland floor (Tables 4.1 and 4.2). Most introduced species were positively associated with higher levels of dark and light phase PAR. The main exception to this trend was *Hyacinthoides non-scripta*. The negative relationship between this vernal species, which capitalises on light phase irradiance, and dark phase PAR is predictable. However, the negative association with light phase PAR suggests that factors other than light intensity are more important to the establishment of this species. The tolerance and positive association of *Hyacinthoides* with high litter cover (Figures 4.24 and 4.25) probably determines niche colonisation by this species. Although the light climate variables are more allied with axis 1 than axis 2 (Figure 4.24), litter and the opposing mineralisable nitrogen are most

closely associated with axis 1 and together have a more wide reaching influence on the vegetation (Figure 4.24). Thinning effects were also evident at the species level, with *Brachypodium sylvaticum, Stellaria holostea* and *Viola riviniana* growing at higher densities in thinned plots, and *Campanula trachelium* and *Primula vulgaris* only germinating in thinned plots, in both years (Figures 4.26 and 4.28).

Although thinning and fertilisation treatments were not, in isolation, the main determinants of plant distribution in this experiment (Sections 4.3.3.1 and 4.3.3.2), their effects in combination and interaction were also investigated. Newly colonising species, including introductions, were favoured in thinned and fertilised plots. This is illustrated at the community level by the positive response of the total density of all introduced species to both thinning and fertilisation (Tables 4.1 and 4.2). At the individual species level, *Primula vulgaris* only germinated in thinned and fertilised plots in the first year (Figures 4.26 and 4.27). Certain introduced species appeared to have a particularly strong association with certain thinned and fertilised plots. This was particularly evident for *Silene dioica* and *Brachypodium sylvaticum* in the first year and for *Silene* and *Viola riviniana* in the second, in the spontaneous vegetation ordinations where introduced species, along with other significant environmental variables, were used to constrain the ordinations (Figures 4.21 and 4.25). Thinning and fertilisation in combination appears to encourage the establishment of introduced species within available niches. Of these species, only *Viola riviniana* occurred at higher densities in both thinned and fertilised plots in both seasons (Figures 4.26-4.29).

The design of Experiment 2 allowed investigation of interactions between soil fertility and light intensity, which were not possible in Experiment 1. It was originally hypothesised by Cohn (1994) that this interaction at establishment could be crucial to the development of target communities. It was thought that certain spontaneous species, such as *Urtica dioica*, which are able to persist in dense shade if soil fertility is significantly high, could occupy valuable niche space and provide competition for resources. However, it was also hypothesised that species such as *Urtica* could act as a surrogate canopy for introduced woodland herbs, ameliorating niche microclimates and perhaps enhancing their establishment. The behaviour of *Urtica* at community level (Figures 4.14 and 4.24) in Experiment 2 indicates that it may be performing the function of a surrogate canopy, and enhancing the establishment of certain introductions. Density data were not collected for the spontaneous species, but were for the introduced species.

These data allowed detection of an interaction between soil fertility and light intensity (as represented by the treatment variables). *Campanula trachelium* and *Stellaria holostea* densities in the first year both show a significant interaction (Table 4.1 and Figure 4.30). The positive interaction between light and fertility significantly enhances the success of these species in density terms, over and above that which could be attributed to either factor acting alone (Figure 4.30). However, a significant interaction was also detected acting on dark phase PAR (Figure 4.30). Plots that were thinned and fertilised exhibited a higher summer light regime than those that were only thinned; thinning always produced a higher light climate than control plots. This probably represents a plot position effect, rather than a true interaction between light and fertility, where thinning of a less dense background canopy coincides with fertility treatment. This means that the similar interaction patterns evident on the densities of *Campanula trachelium* and *Stellaria holostea* (Figure 4.30) may be an artefact of the background conditions in colonised plots. The strong association of these species with position along the x-axis of the experiment in 1998, perhaps reinforces a plot position effect (Figure 4.20).

4.5 Conclusions

- Woodland ground flora can be successfully introduced into existing secondary woodland communities, supporting the findings of Cohn (1994), without use of a herbicide pretreatment and into relatively vigorous established vegetation.

- The larger plot size and 'whole wood' buffer zone in this experiment largely overcame the edge effects evident in Experiment 1.

- Experimental design was successful in detecting interactions between soil fertility and light intensity.

- Experimental design was partly effective in isolating and describing effects related to the main north-westerly slope of the experiment. However, this design could not account for slope effects on the secondary south-westerly slope. These secondary slope effects, which turned out to be significant in relation to litter and mineralisable nitrogen, apparently had a greater influence on the vegetation than the main slope effects, which were related to soil pH.

- Background spatial variation in percentage litter cover, created partly by slope effects, was a major determinant of field layer development. Mineralisable nitrogen

was inversely related to this variable, and probably largely a consequence of it. The litter–nitrogen gradient, related to the secondary slope in the experiment, provided germination niches. The success of establishment of the introduced species in these niches was enhanced by thinning and fertilisation treatments.

- Thinning and fertilisation appeared to encourage the establishment of introduced species within available niches. However, the effects of fertilisation treatment were difficult to detect at the community level and the benefits to the wider target community arguable. The major soil fertility influence (i.e. mineralisable nitrogen) is likely to have been determined largely by the spatial distribution of litter, and was not apparently influenced by thinning treatment.

- Background soil fertility is perhaps close to optimum for ground flora enhancement at Nedge Hill. If fertility levels had proved an obstacle to ground flora enhancement, it seems unlikely that, in practice, fertility levels could readily be manipulated in a direction or on a scale likely to be beneficial.

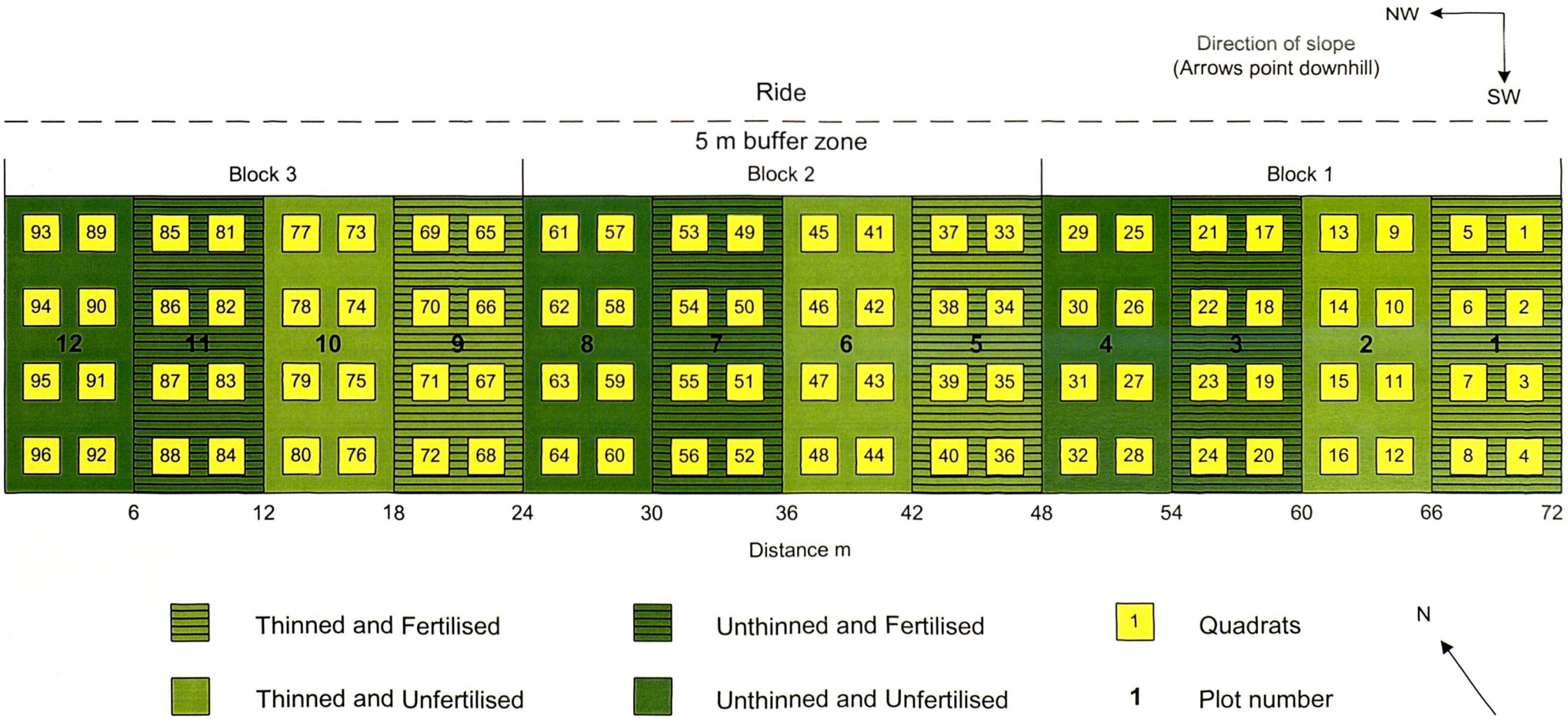


Figure 4.1 Layout of Experiment 2: the light intensity and soil fertility manipulation experiment at Nedge Hill, Telford. Treatment plot and quadrat locations are shown. (Figures 4.2-4.13, 4.16-4.17 conform to this layout).

Plate 4.1 Unthinned plots 3 and 4 (Figure 4.1) within Experiment 2: the soil fertility and light manipulation experiment at Nedge Hill on establishment, 14/02/98. The spontaneous field layer is a patchy vegetation characterised by competitive ruderal and woodland species. Fertility treatment split plots can be seen marked out with tape. Bags filled with the seed / sand mix can be seen placed in plots ready for sowing.

Plate 4.2 Thinned plots 9 and 10 (Figure 4.1) within Experiment 2 on establishment, 15/02/98. Fertility treatment split plots can be distinguished as above. Sowing bags are also visible.

Plate 4.3 Second season (01/06/99) vegetation response within unthinned plots 3 and 4 (Figure 4.1) of Experiment 2. The sparse field layer is characterised by bryophytes and *Fraxinus excelsior* seedlings with scattered competitive ruderal and woodland species. The introduced species *Brachypodium sylvaticum* and *Hyacinthoides non-scripta* occur frequently.

Plate 4.4 Detail of the second season (01/06/99) vegetation response within thinned plots 1 and 2 (Figure 4.1) of Experiment 2. The field layer is as described above, however, introduced species form a larger and more consistent component of the vegetation under a thinned canopy. *Galium odoratum* and *Brachypodium sylvaticum* are visible in this case.

Plate 4.5 Second season (01/06/99) vegetation response within thinned plots 1 and 2 (Figure 4.1) of Experiment 2. The vigorous field layer comprises a mosaic of tall and short herb forms, characterised by bryophytes, tree seedlings, spontaneous competitive ruderal and woodland species plus introduced species, such as *Silene dioica* and *Viola riviniana*.

Plate 4.6 Detail of the second season (01/06/99) vegetation response within thinned plots 9 and 10 (Figure 4.1) of Experiment 2. *Silene dioica* and *Scrophularia nodosa* contribute to the structure within the field layer.

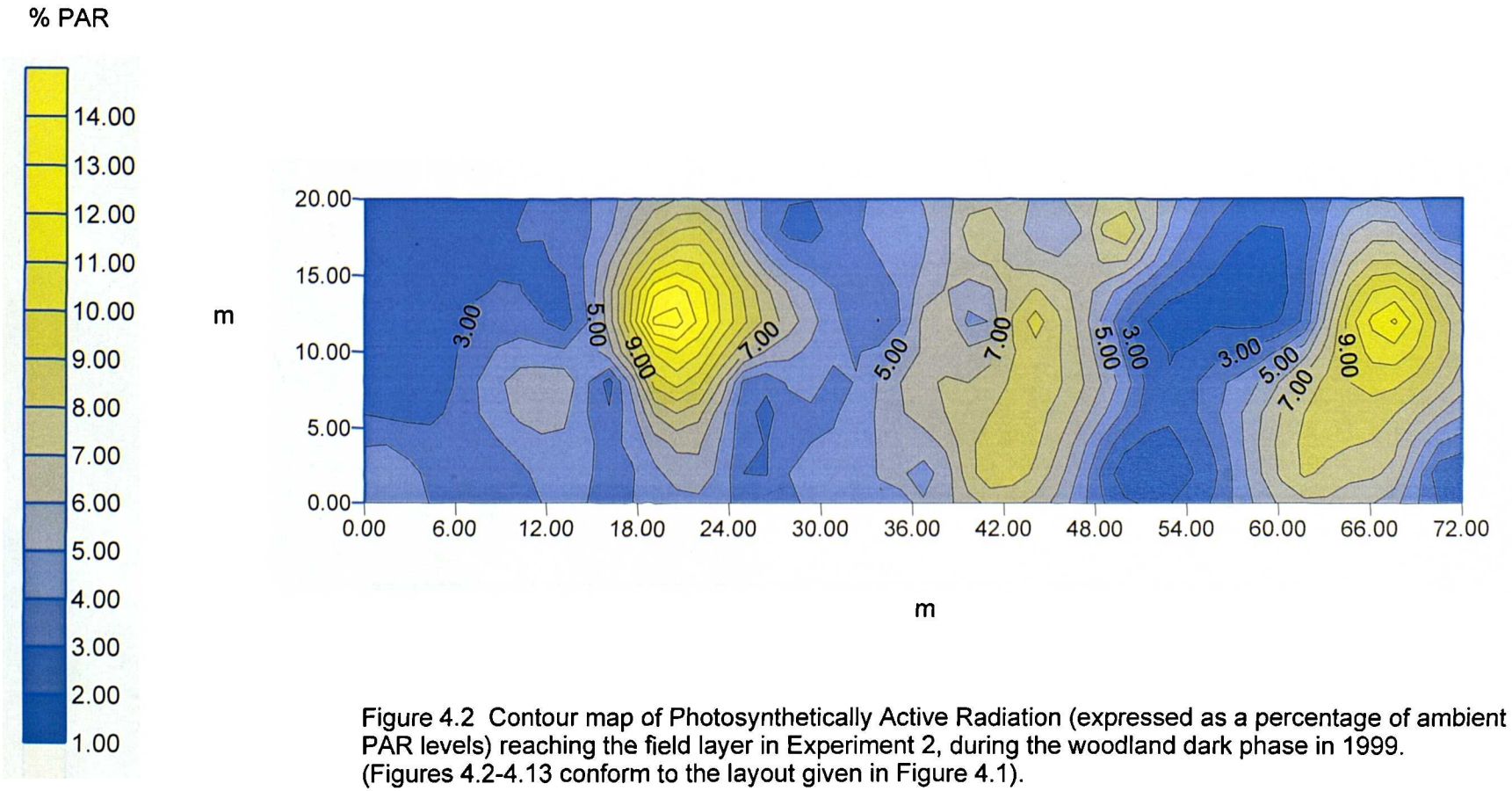


Figure 4.2 Contour map of Photosynthetically Active Radiation (expressed as a percentage of ambient PAR levels) reaching the field layer in Experiment 2, during the woodland dark phase in 1999. (Figures 4.2-4.13 conform to the layout given in Figure 4.1).

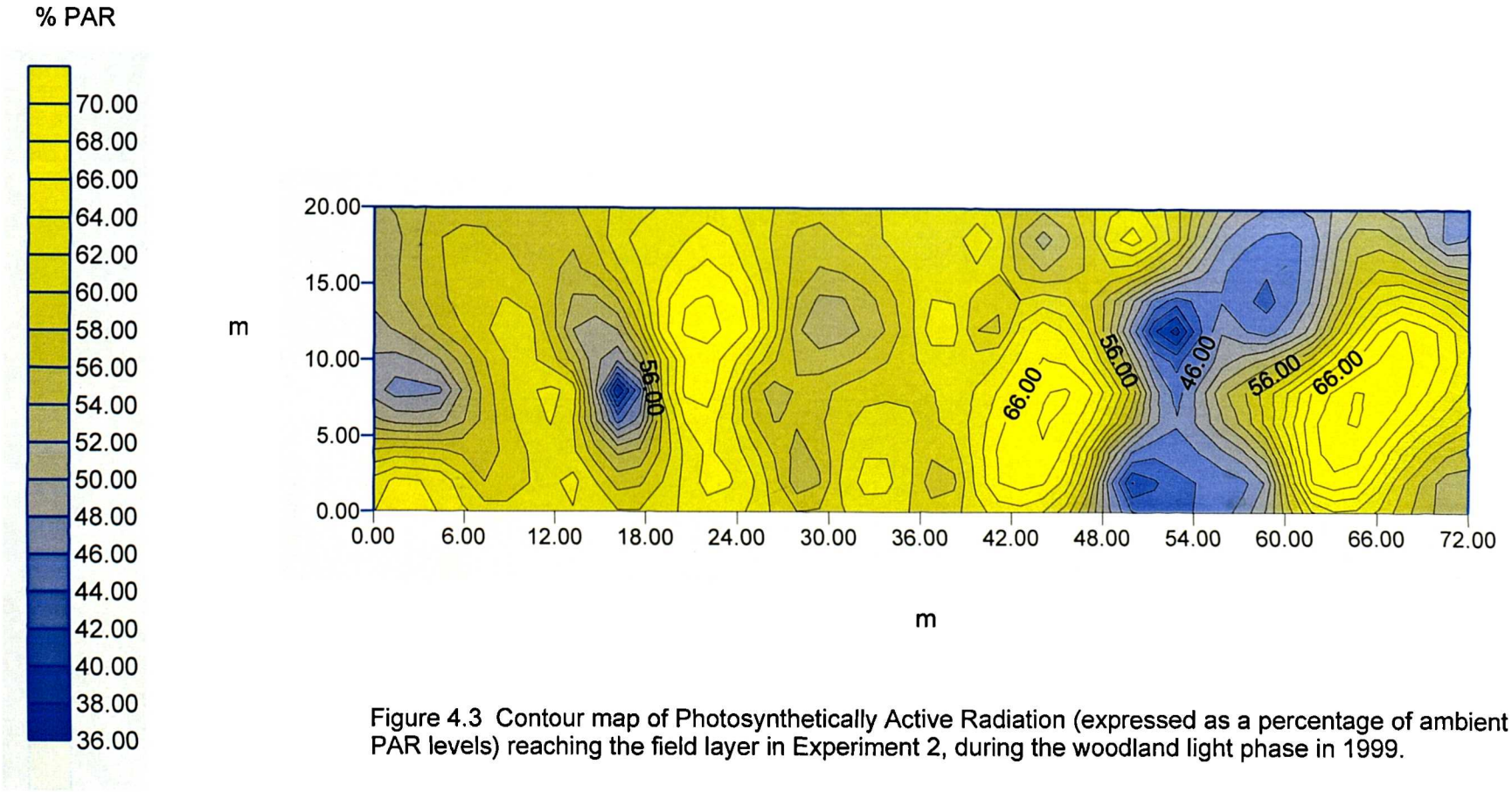


Figure 4.3 Contour map of Photosynthetically Active Radiation (expressed as a percentage of ambient PAR levels) reaching the field layer in Experiment 2, during the woodland light phase in 1999.

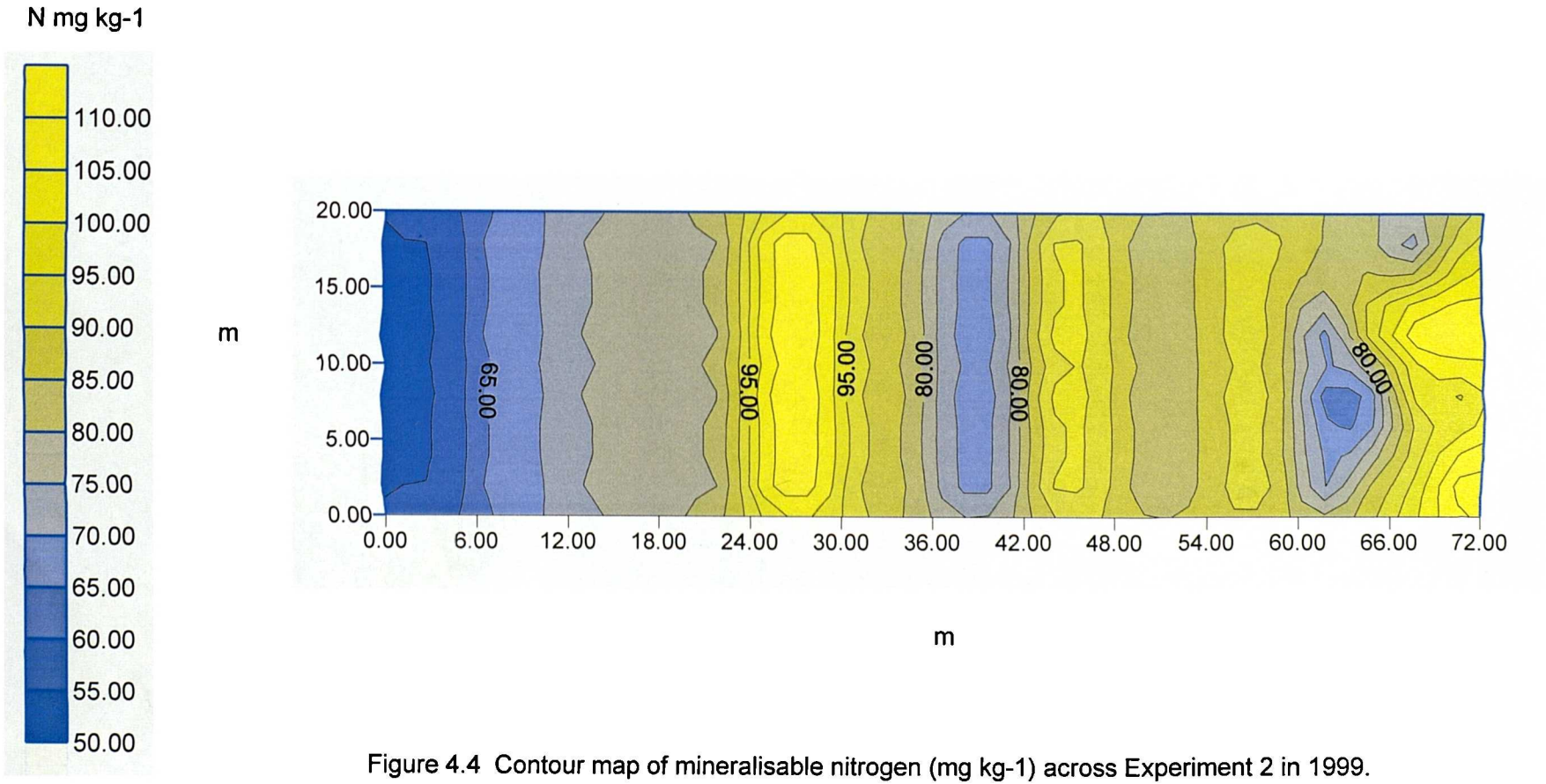


Figure 4.4 Contour map of mineralisable nitrogen (mg kg-1) across Experiment 2 in 1999.

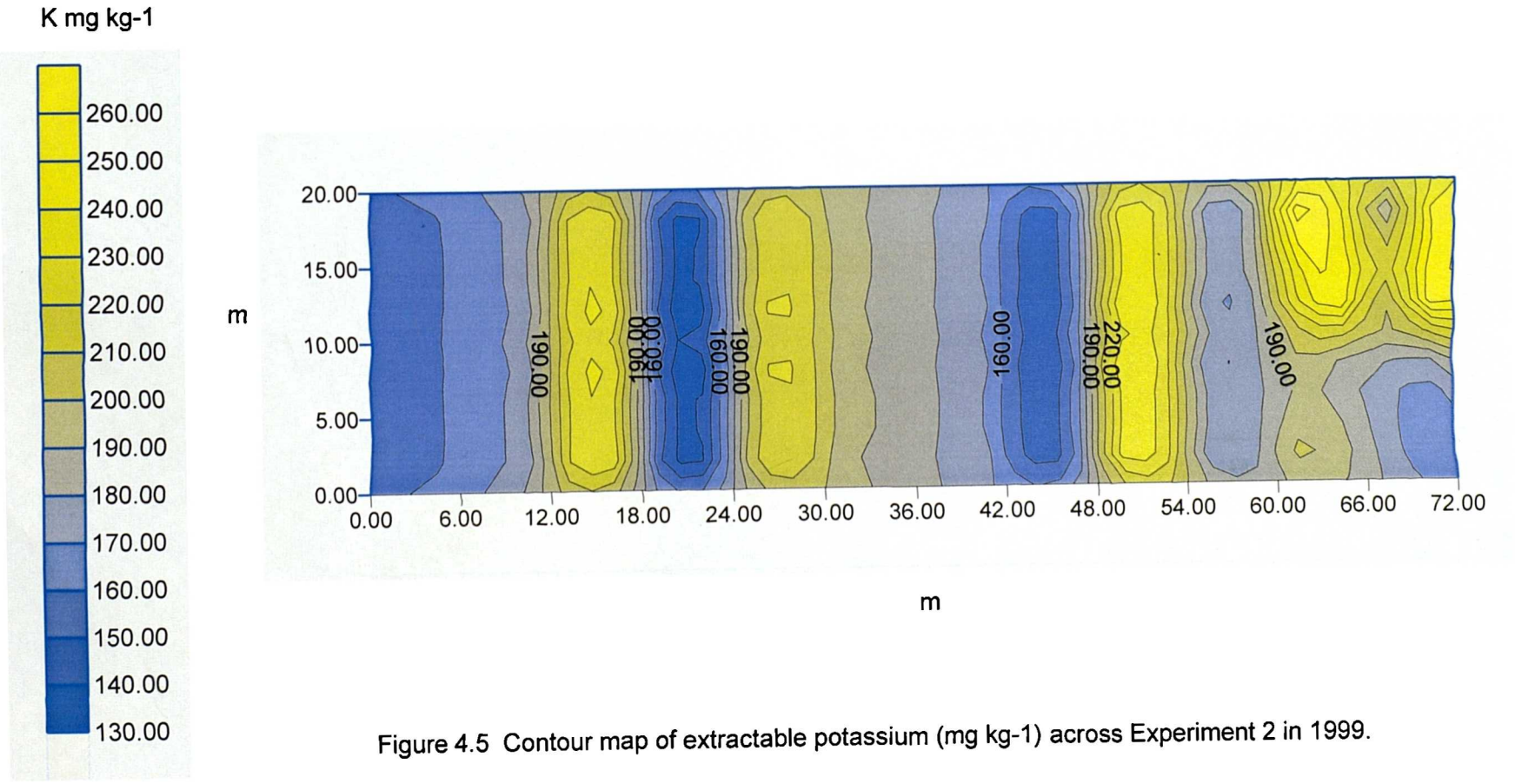


Figure 4.5 Contour map of extractable potassium (mg kg-1) across Experiment 2 in 1999.

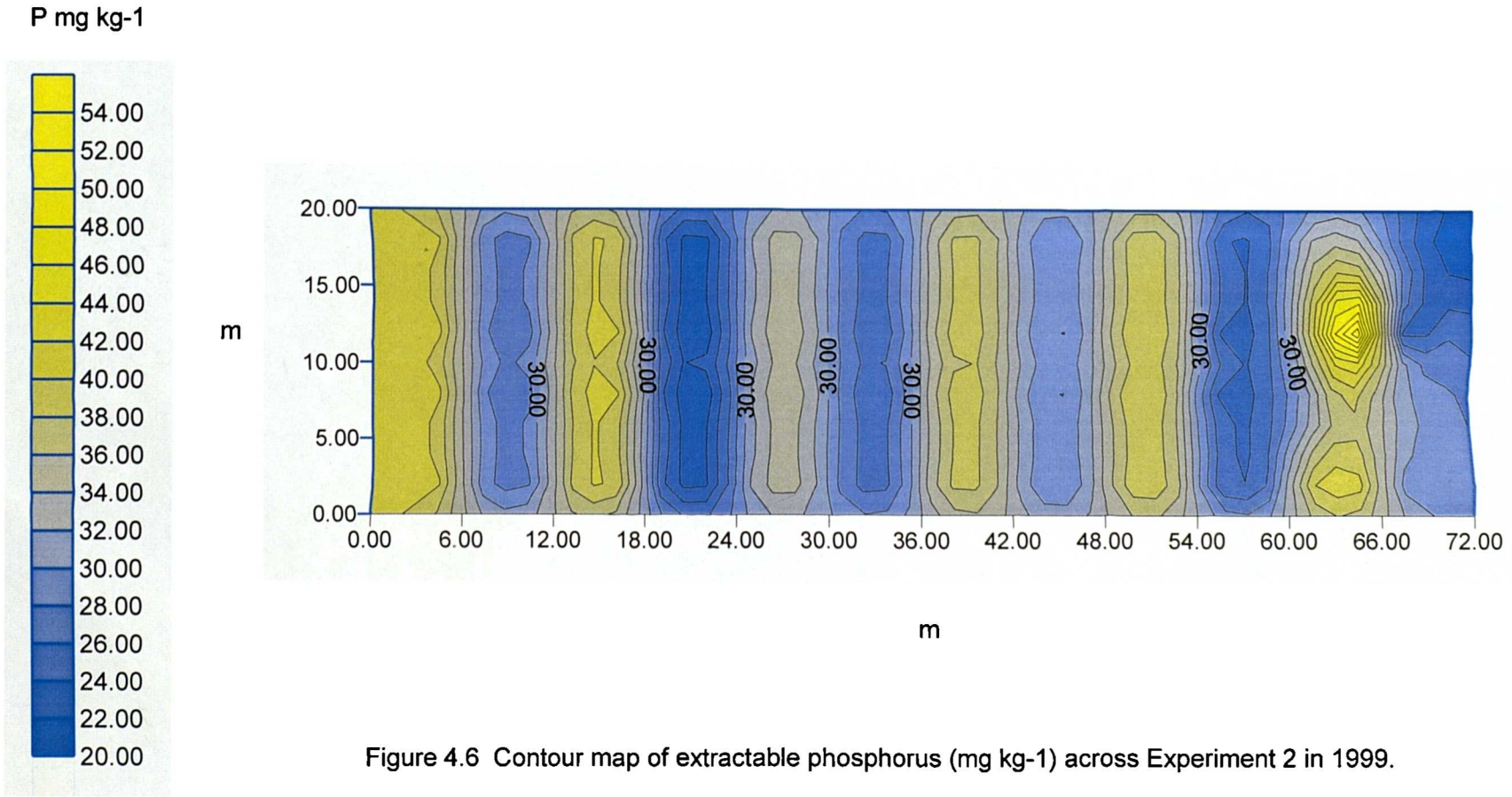


Figure 4.6 Contour map of extractable phosphorus (mg kg-1) across Experiment 2 in 1999.

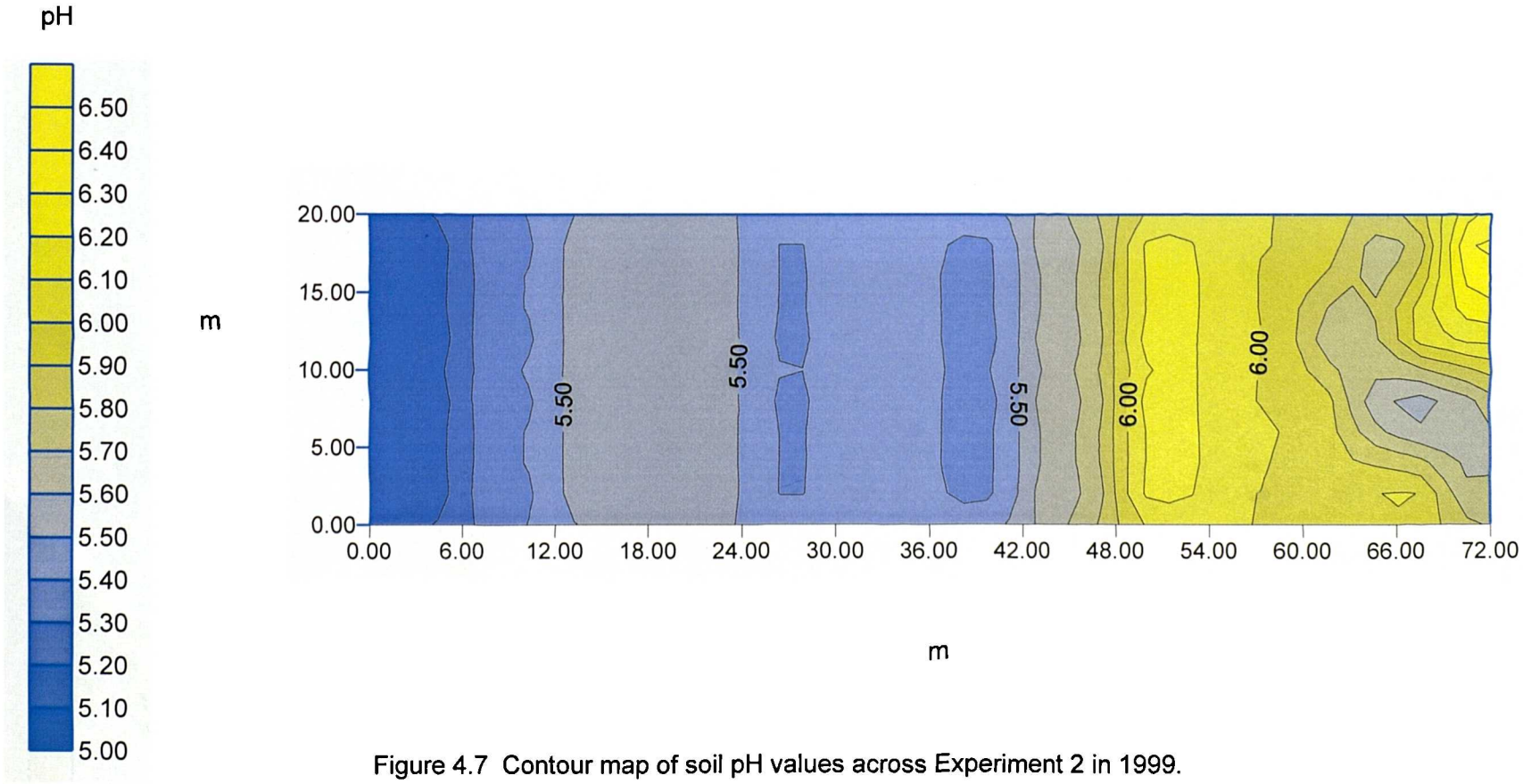


Figure 4.7 Contour map of soil pH values across Experiment 2 in 1999.

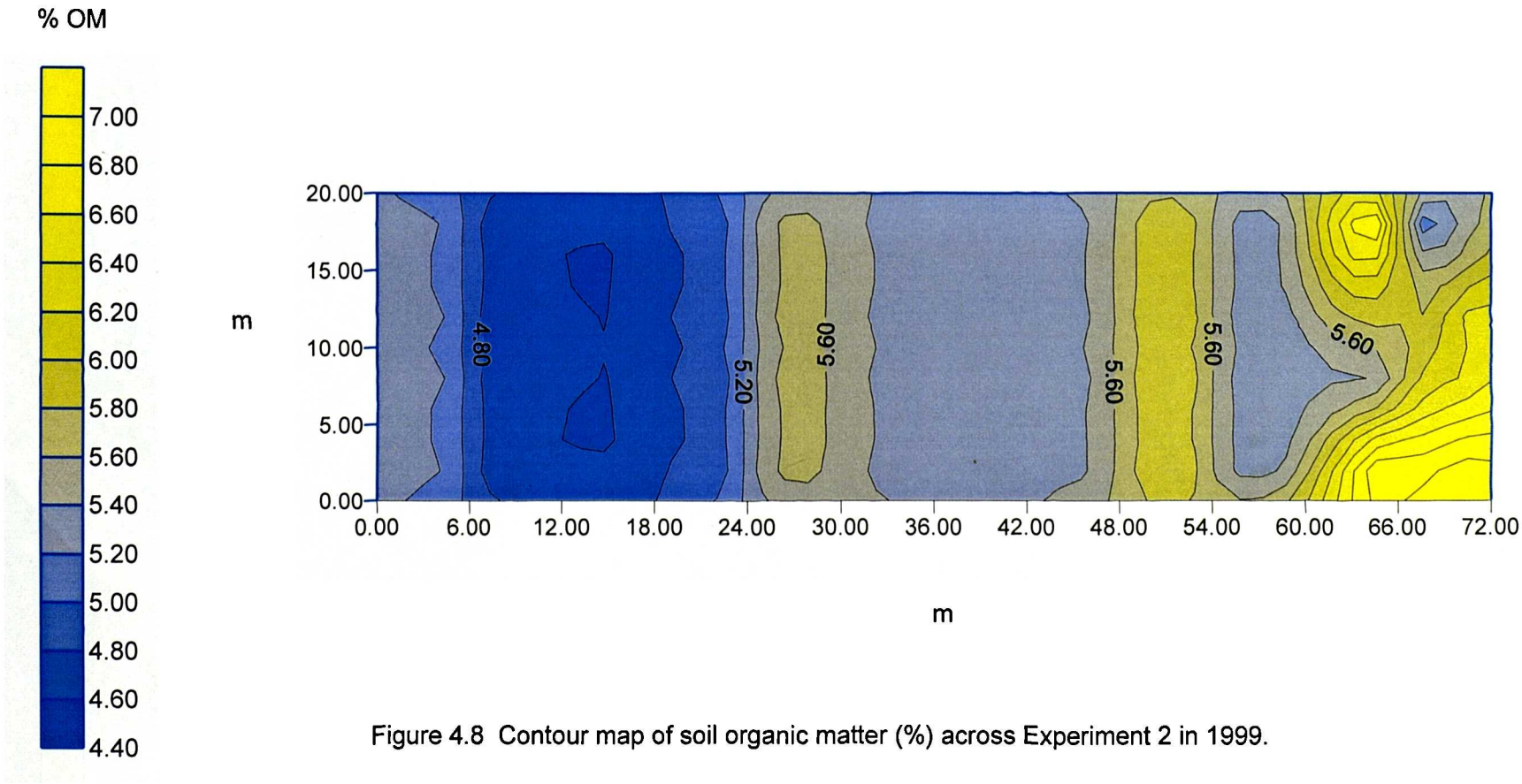


Figure 4.8 Contour map of soil organic matter (%) across Experiment 2 in 1999.

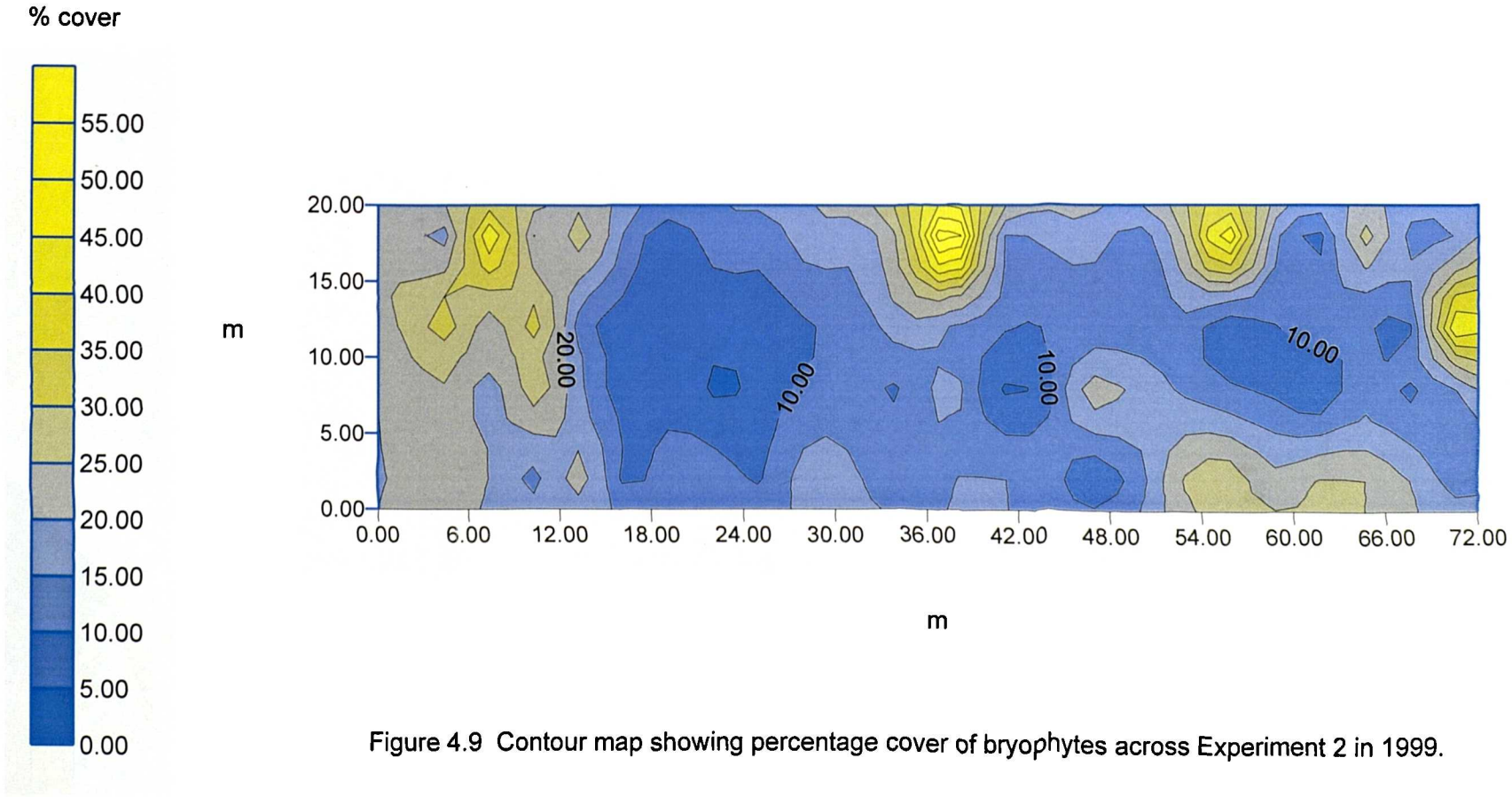


Figure 4.9 Contour map showing percentage cover of bryophytes across Experiment 2 in 1999.

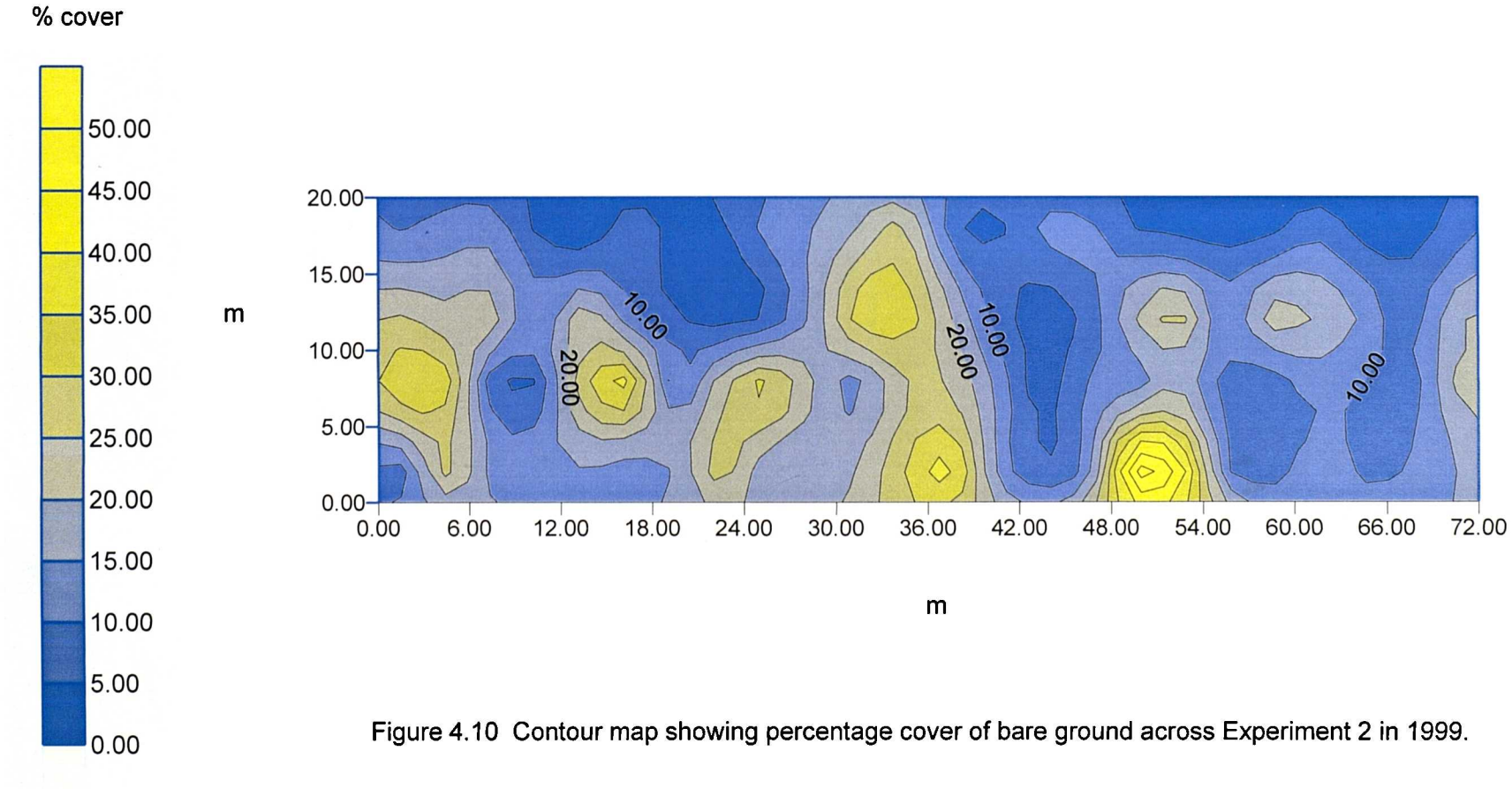


Figure 4.10 Contour map showing percentage cover of bare ground across Experiment 2 in 1999.

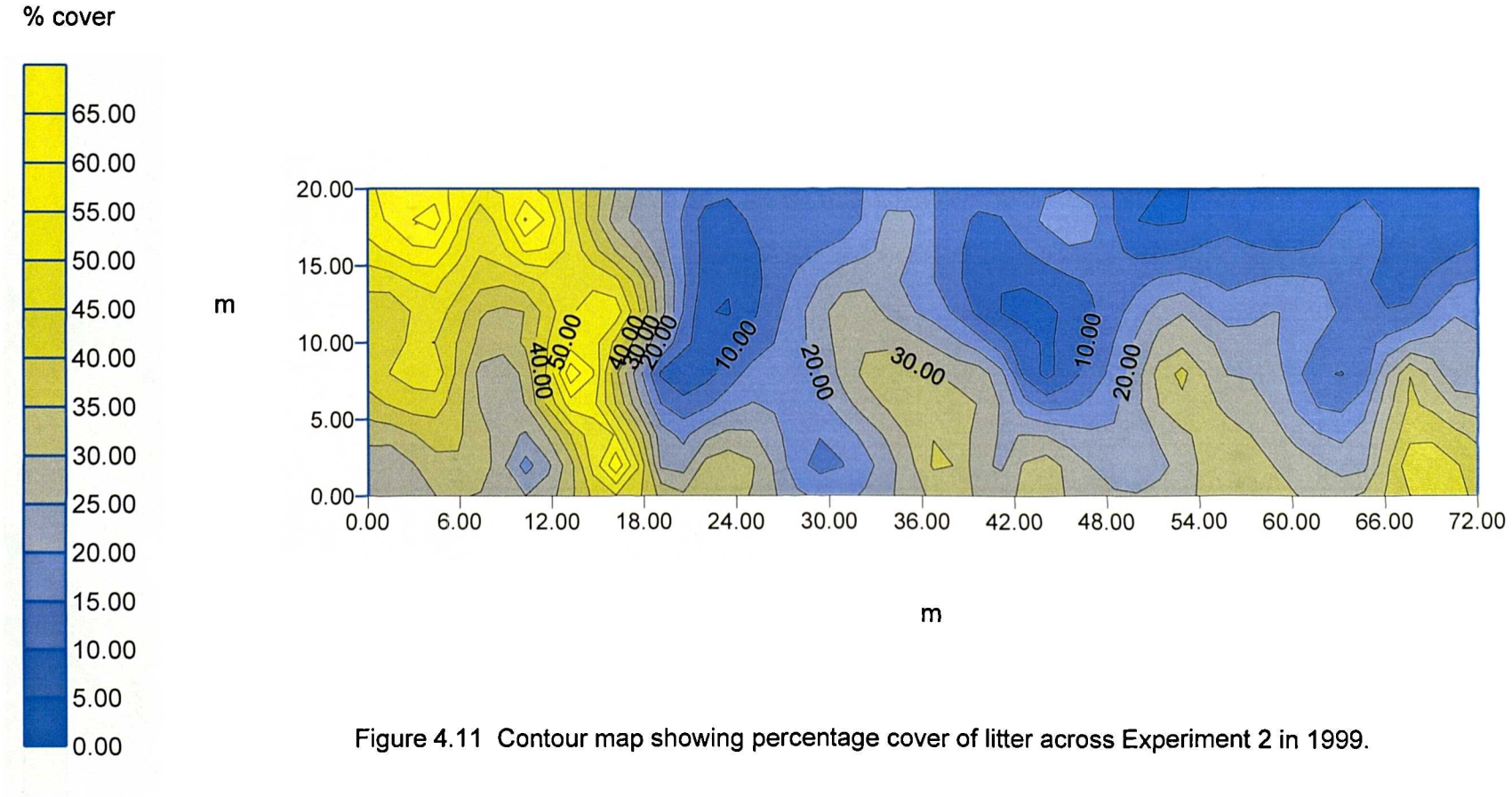


Figure 4.11 Contour map showing percentage cover of litter across Experiment 2 in 1999.

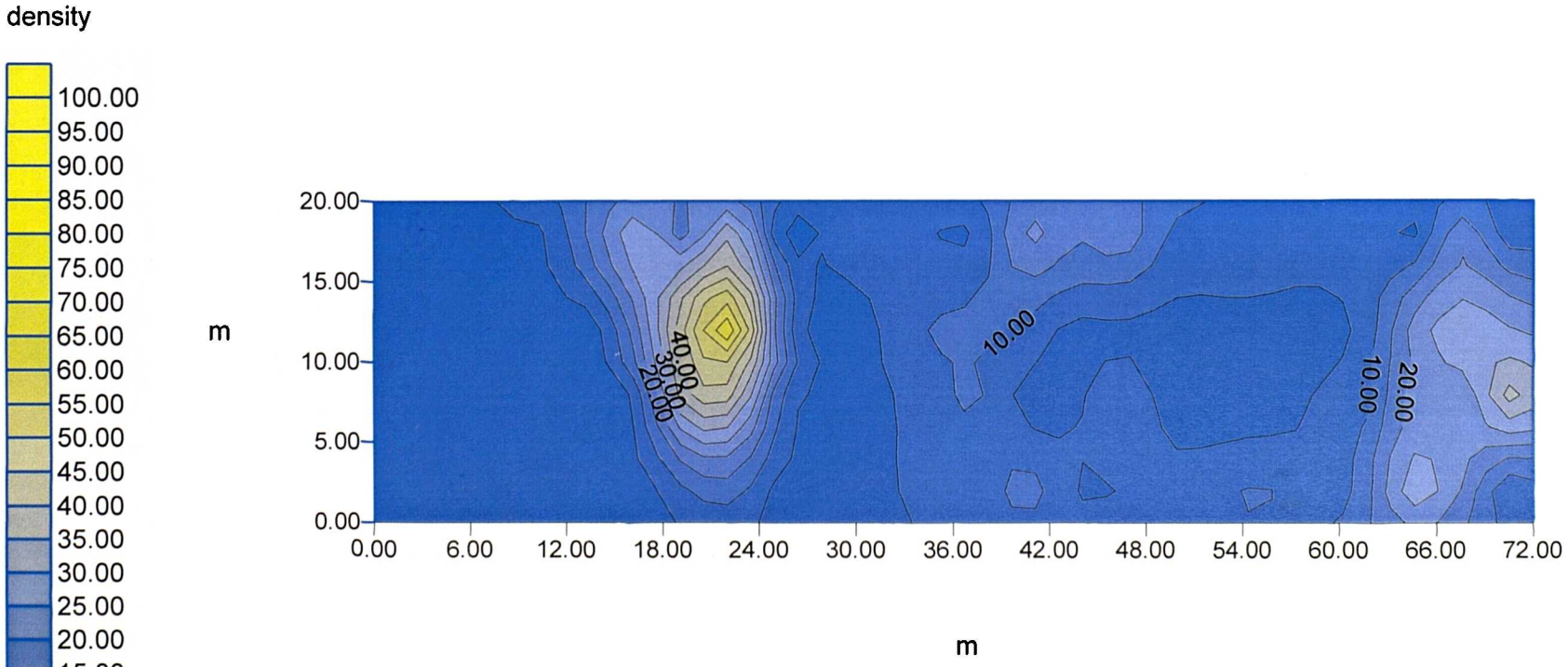


Figure 4.12 Contour map showing the density distribution of introduced species across Experiment 2 in 1998.

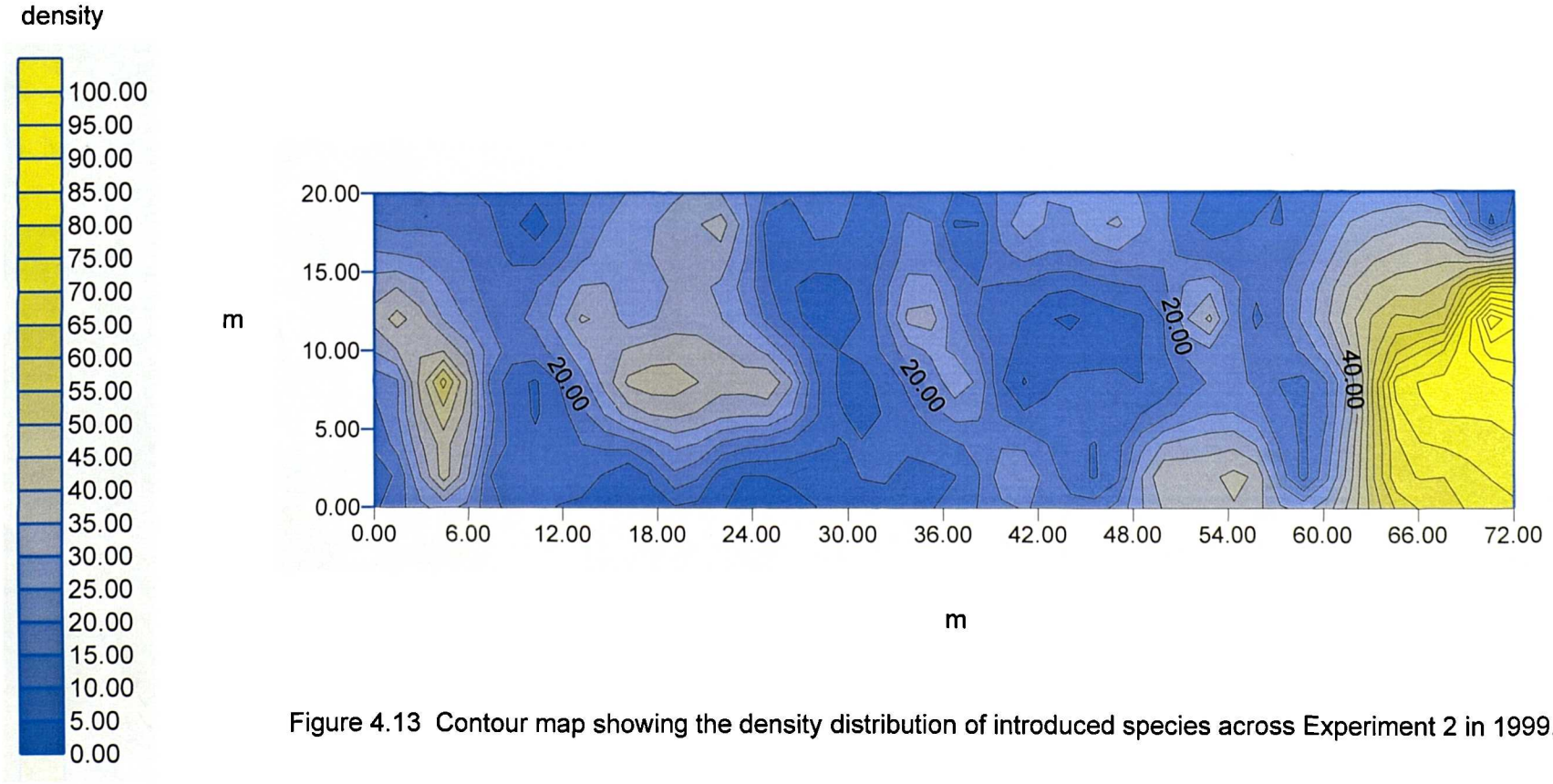


Figure 4.13 Contour map showing the density distribution of introduced species across Experiment 2 in 1999.

Table 4.1: ANOVA Table showing treatment significant variables in Experiment 2.

		Mean Squares of variables with significance levels			
Source of variation	d.f.	PARD	PARL	Canopy 98t	Canopy 99t
Block	2	2.911 ns	258.5 **	0.1262 ns	0.2094 *
Light	1	254.2 ***	805.7 ***	1.06 ***	1.752 ***
Fertility	1	33.66 *	179.9 ns	0.03682 ns	0.00691 ns
Light*Fertility	1	28.79 *	35.19 ns	0.00199 ns	0.07593 ns
Residual	90	5.791	52.61	0.05112	0.05144

		Mean Squares of variables with significance levels			
Source of variation	d.f.	Bryophyte 98t	Bareground 99	Litter 98	DenIntro 98t
Block	2	0.05854 ns	59.0 ns	8748.6 ***	3.173 ns
Light	1	0.03691 ns	672.0 *	1372.6 *	79.64 ***
Fertility	1	0.0916 *	748.2 *	341.3 ns	19.87 ***
Light*Fertility	1	0.01591 ns	0.2 ns	8.8 ns	2.002 ns
Residual	90	0.0196	119.3	281.2	1.827

		Mean Squares of variables with significance levels			
Source of variation	d.f.	DenIntro 99t	Brac sylv 98t	Brac sylv 99	Camp trac 98t
Block	2	38.68 ***	3.95 *	163.72 *	0.7539 *
Light	1	28.67 ***	51.86 ***	1449.3 ***	3.643 ***
Fertility	1	0.412 ns	9.044 **	23.01 ns	1.842 **
Light*Fertility	1	7.255 ns	0.009 ns	14.26 ns	1.842 **
Residual	90	2.634	1.218	35.64	0.2111

		Mean Squares of variables with significance levels			
Source of variation	d.f.	Camp trac 99t	Prim vulg 99t	Sile dioi 98t	Sile dioi 99t
Block	2	0.08424 ***	0.0652 ns	0.4951 ns	2.382 ***
Light	1	0.1573 ***	0.6415 *	1.46 *	0.1081 ns
Fertility	1	0.02273 ns	0.0355 ns	0.2779 ns	0.1081 ns
Light*Fertility	1	0.02273 ns	0.0002 ns	1.052 ns	2.581 ***
Residual	90	0.01392	0.1032	0.3193	0.2403

		Mean Squares of variables with significance levels			
Source of variation	d.f.	Stel holo 98t	Stel holo 99t	Viol rivi 98t	Viol rivi 99t
Block	2	0.708 *	2.712 ***	1.498 ***	1.048 ns
Light	1	5.538 ***	1.706 *	5.014 ***	3.977 ***
Fertility	1	2.0015 **	0.2945 ns	3.245 ***	2.627 **
Light*Fertility	1	1.255 *	0.0381 ns	0.071 ns	0.266 ns
Residual	90	0.2246	0.26	0.288	0.3623

		Mean Squares of soil variables with significance levels		
Source of variation	d.f.	Ext P	OMt	pH
Block	2	2.19 ns	0.8299 ***	0.2892 *
Light	1	0.45 ns	0.01042 ns	0.00317 ns
Fertility	1	478.5 ***	0.04183 ns	0.03467 ns
Light*Fertility	1	0.65 ns	0.4318 *	0.005 ns
Residual	6	12.13	0.03268	0.0421

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively. ns: not significant. t: transformed data.

98/99: year. Den Intro: density of introduced species. OM: soil organic matter (%).

All density data for individual species denoted by abbreviated Latin names (Section 2.7.2.2).

Table 4.2: Table of means of treatment significant variables in Experiment 2.

	Means of variables per light treatment replicate			
Light treatment	PARD	PARL	Canopy 98t	Canopy 99t
Thinned	6.9	60.7	80.3	68.4
Unthinned	3.6	54.9	93.7	89.2
Standard Error	0.35	1.05	0.033	0.033

	Means of variables per light treatment replicate			
Light treatment	Bareground 99	Litter 98	Den Intro 98t	Den Intro 99t
Thinned	12.4	27.7	16.1	32.8
Unthinned	17.7	35.2	4.1	19.8
Standard Error	1.6	2.4	0.2	0.23

	Means of variables per fertility treatment replicate				
Fertility treatment	PARD	Bryophyte 98t	Bareground 99	Den Intro 98t	Ext P
Fertilised	5.8	19.1	12.2	13.0	25.4
Unfertilised	4.7	14.6	17.8	7.2	38.0
Standard Error	0.35	0.02	1.6	0.2	1.4

t: ANOVA performed on transformed data. 98/99: year.

Den Intro: density of introduced species.

All density data for individual species denoted by abbreviated Latin names (Section 2.7.2.2).

Table 4.3: ANOVA Table showing block significant variables in Experiment 2. (NB. ANOVA results from block significant variables which are also treatment significant are given in Table 4.1).

		Mean Squares of variables with significance levels			
Source of variation	d.f.	Axis1 99	Axis2 98	Axis2 99t	Bareground 98t
Block	2	13.52 ***	9.866 ***	0.5925 *	0.279 ***
Light	1	0.0759 ns	0.0721 ns	0.044 ns	0.00012 ns
Fertility	1	0.5677 ns	0.2648 ns	0.0792 ns	0.05595 ns
Light*Fertility	1	0.4765 ns	0.7609 ns	0.9491 ns	0.06597 ns
Residual	90	0.7538 ns	0.8352 ns	0.171 ns	0.02908 ns

		Mean Squares of variables with significance levels			
Source of variation	d.f.	Litter 99	woodybrash98t	woodybrash99t	Hyac nons 99t
Block	2	3040.0 ***	0.03586 *	0.1002 ***	50.31 ***
Light	1	565.5 ns	0.02734 ns	0.02269 ns	0.337 ns
Fertility	1	635.5 ns	0.00031 ns	0.00033 ns	5.206 ns
Light*Fertility	1	472.6 ns	0.00888 ns	0.01204 ns	1.699 ns
Residual	6	190.8 ns	0.01037 ns	0.006892 ns	3.329 ns

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively. ns: not significant.

t: transformed data. 98/99: year. Den Intro: density of introduced species.

All density data for individual species denoted by abbreviated Latin names (Section 2.7.2.2).

Table 4.4: Table of means of block significant variables in Experiment 2.

	Block means of variables			
Block	Axis 1 99	Axis 2 98	Axis 2 99t	PARL
1	0.02	-0.15	-0.07	54.6
2	0.64	0.62	0.24	60.1
3	-0.66	-0.46	-0.18	58.6
Standard Error	0.15	0.16	0.073	1.28

	Block means of variables			
Block	Canopy 99t	Bareground 98t	Litter 98	Litter 99
1	71.3	18.9	19.8	19.4
2	80.8	6.1	24.2	18.8
3	84.2	7.8	50.4	36.0
Standard Error	0.04	0.03	2.96	2.4

	Block means of variables			
Block	woodybrash98t	woodybrash99t	OMt	pH
1	2.5	1.3	5.7	5.9
2	3.7	2.8	5.4	5.5
3	5.2	4.3	4.8	5.4
Standard Error	0.018	0.015	0.09	0.1

	Block means of variables			
Block	Den Intro 99t	Brac sylv 98t	Brac sylv 99	Camp trac 98t
1	38.6	8.6	12.3	0.5
2	15.1	6.2	8.1	0.1
3	25.1	6.5	8.6	1.1
Standard Error	0.29	0.2	1.06	0.08

	Block means of variables			
Block	Camp trac 99t	Hyac nons 99t	Sile dioi 99t	Stel holo 98t
1	0.4	21.6	0.1	0.8
2	0.1	4.5	0.2	0.3
3	0.1	12.1	1.5	0.8
Standard Error	0.02	0.32	0.09	0.08

	Block means of variables	
Block	Stel holo 99t	Viol rivi 98t
1	1.0	1.0
2	0.2	0.2
3	0.6	1.3
Standard Error	0.09	0.09

t: ANOVA performed on transformed data. 98/99: year.

Den Intro: density of introduced species. OM: soil organic matter (%).

All density data for individual species denoted by abbreviated Latin names (Section 2.7.2.2).

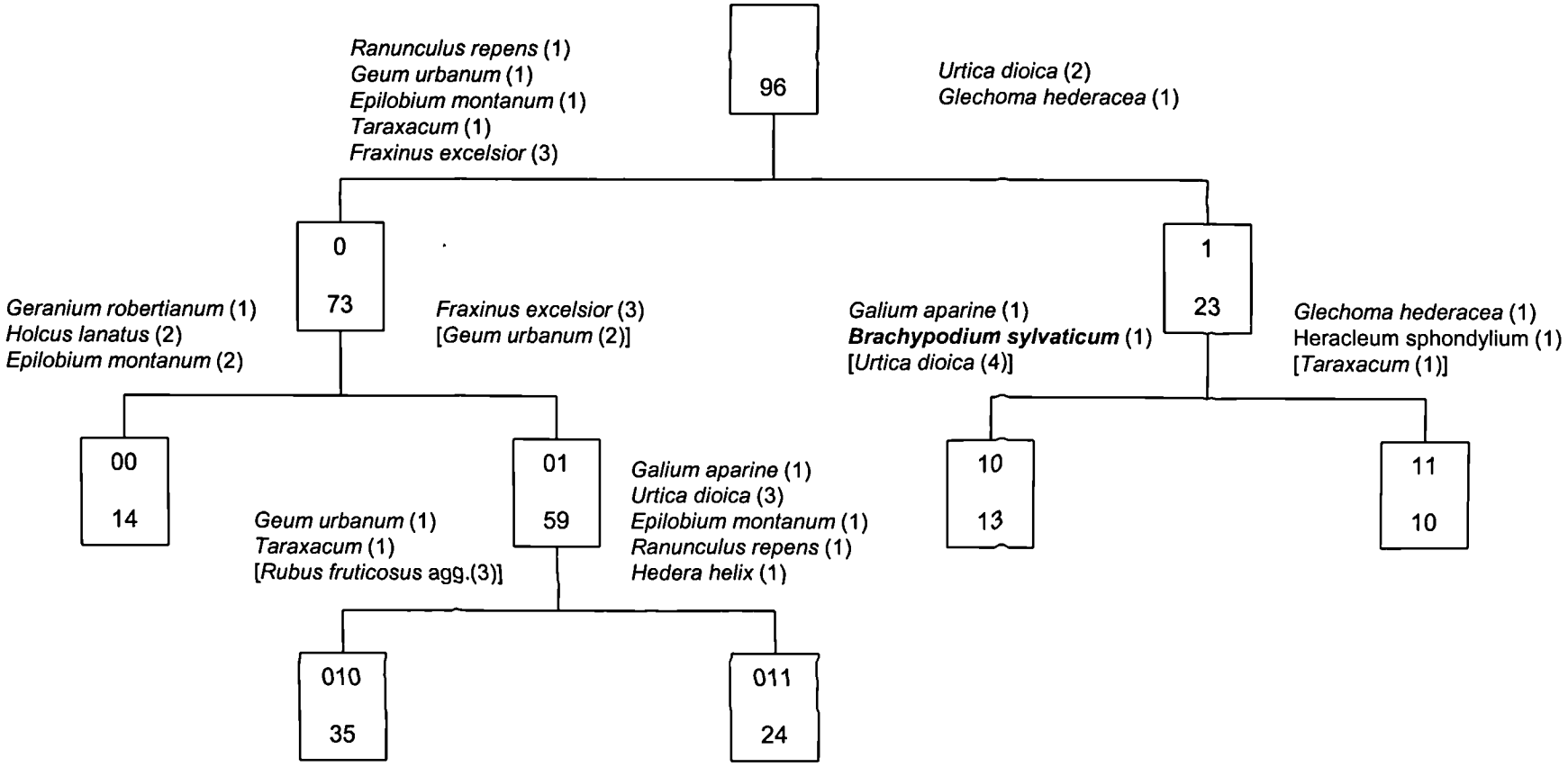


Figure 4.14 TWINSPAN sample classification of the 1998 vegetation data from Experiment 2 (the light and fertility manipulation experiment at Nedge Hill). The upper figure in each box indicates the TWINSPAN group, the lower figure, the number of samples in each group. Indicator species are listed in order of importance, with pseudospecies levels in brackets to indicate abundance. Preferential species, denoted by square brackets, are also given in order of importance, with pseudospecies level in brackets. Introduced species are shown in bold.

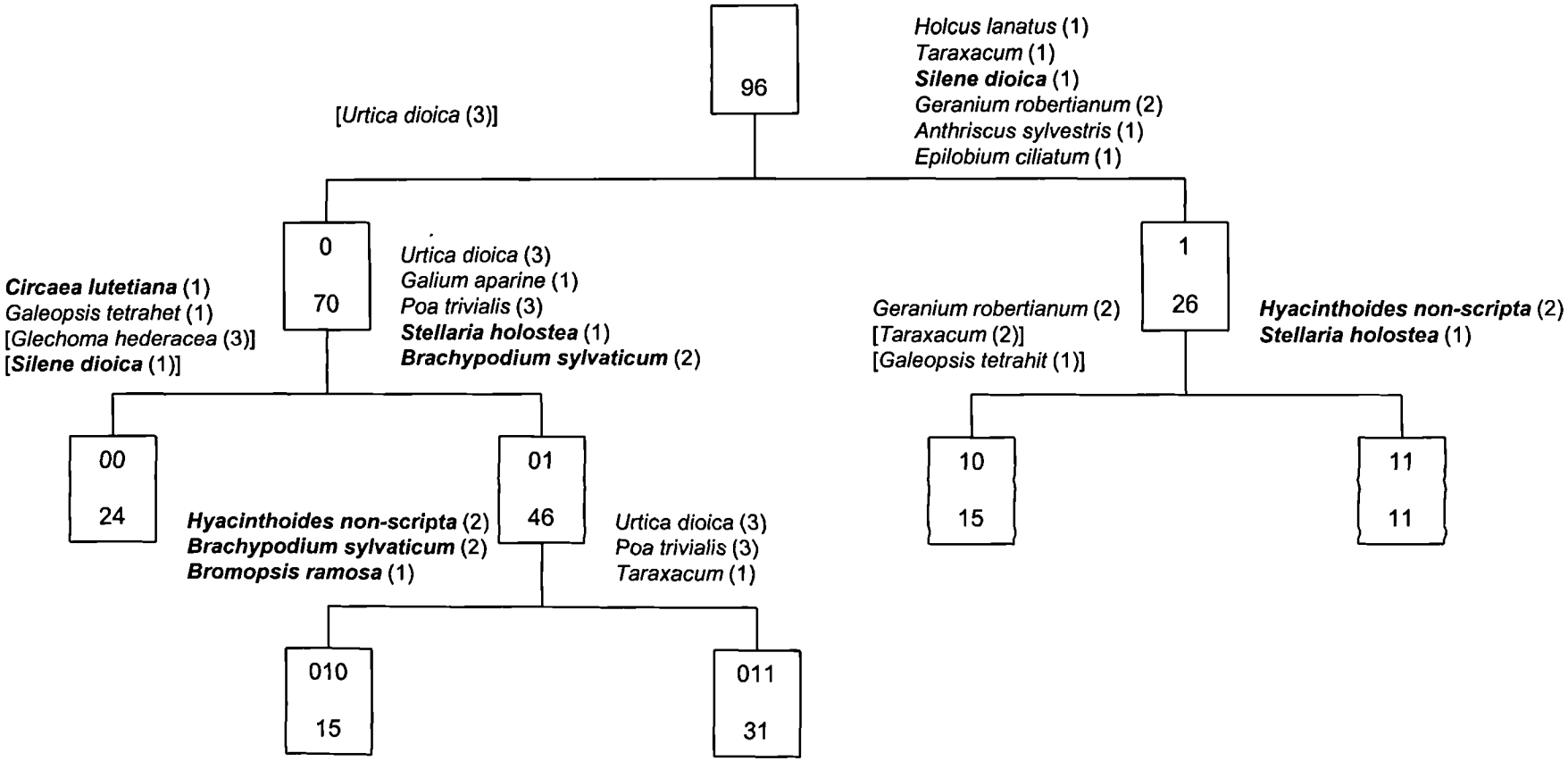


Figure 4.15 TWINSPAN sample classification of the 1999 vegetation data from Experiment 2 (the light and fertility manipulation experiment at Nedge Hill). The upper figure in each box indicates the TWINSPAN group, the lower figure, the number of samples in each group. Indicator species are listed in order of importance, with pseudospecies levels in brackets to indicate abundance. Preferential species, denoted by square brackets, are also given in order of importance, with pseudospecies level in brackets. Introduced species are shown in bold.

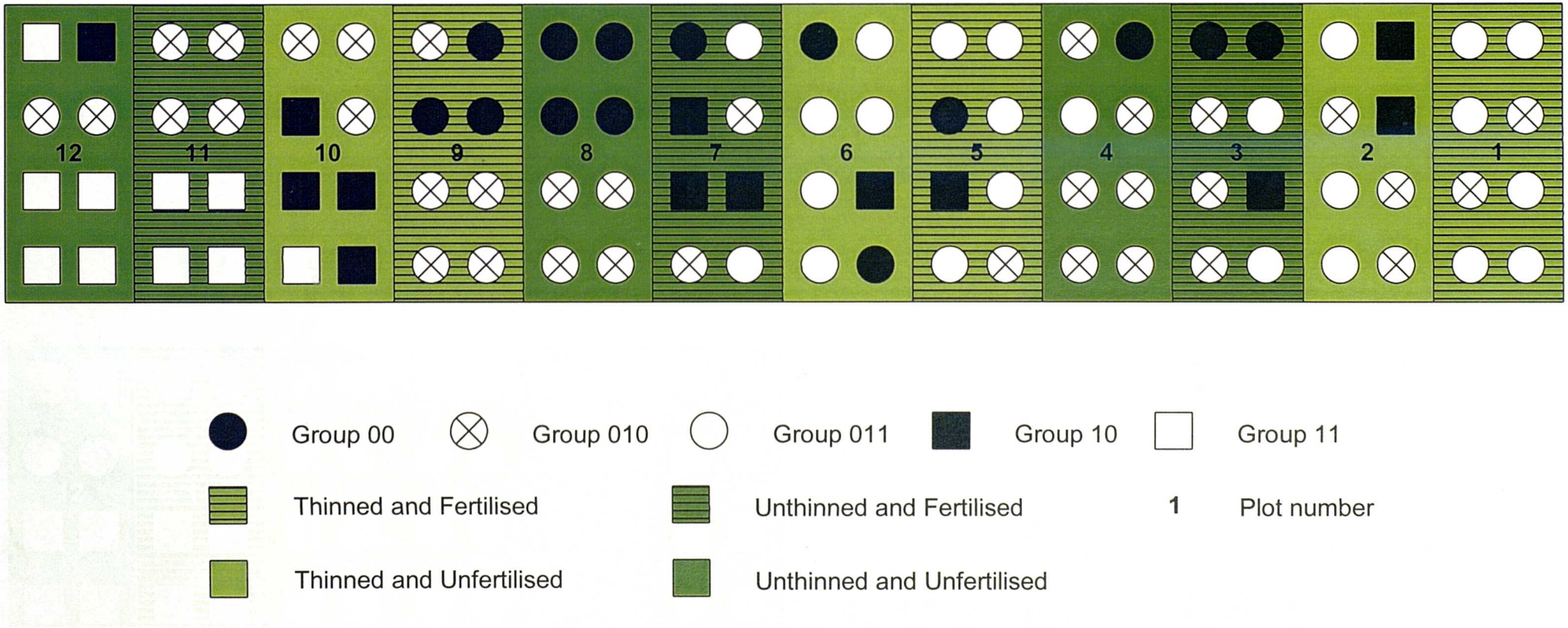


Figure 4.16 Location map of samples recorded in 1998 assigned to TWINSPAN end groups. Treatment plot locations are shown. (Figures 4.16-4.17 conform to the layout given in Figure 4.1).

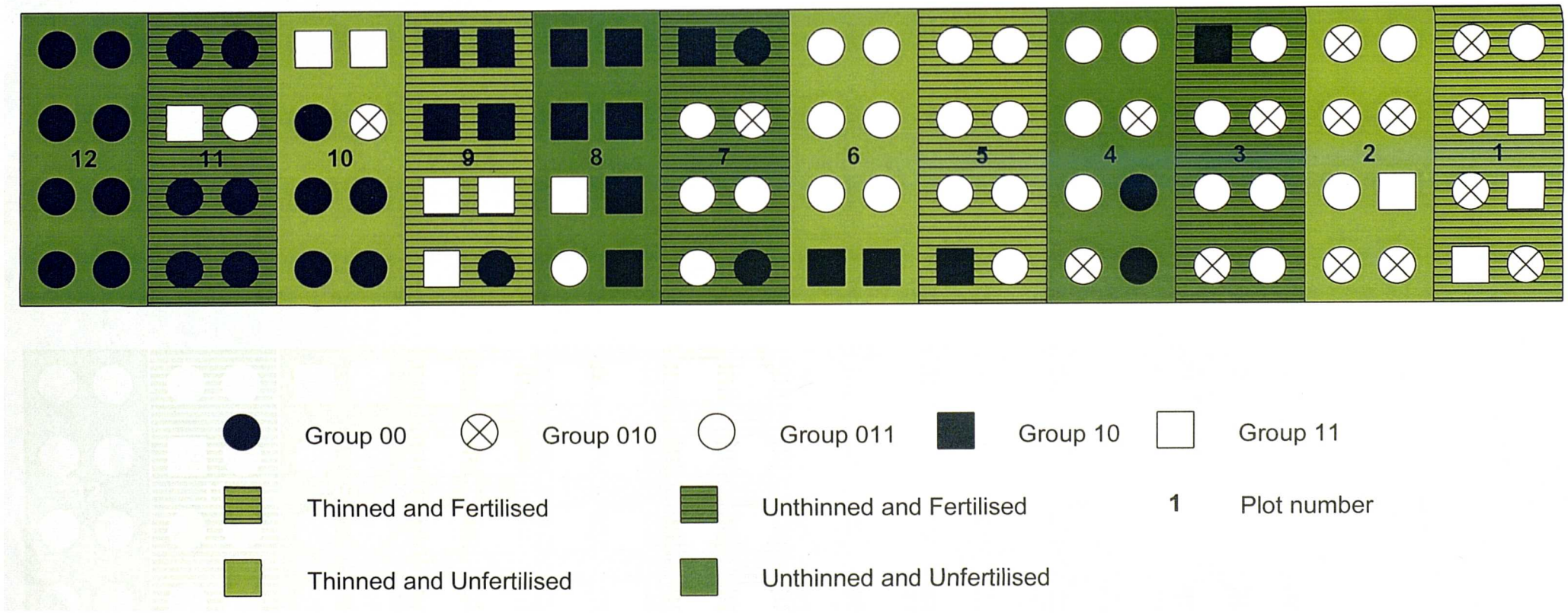
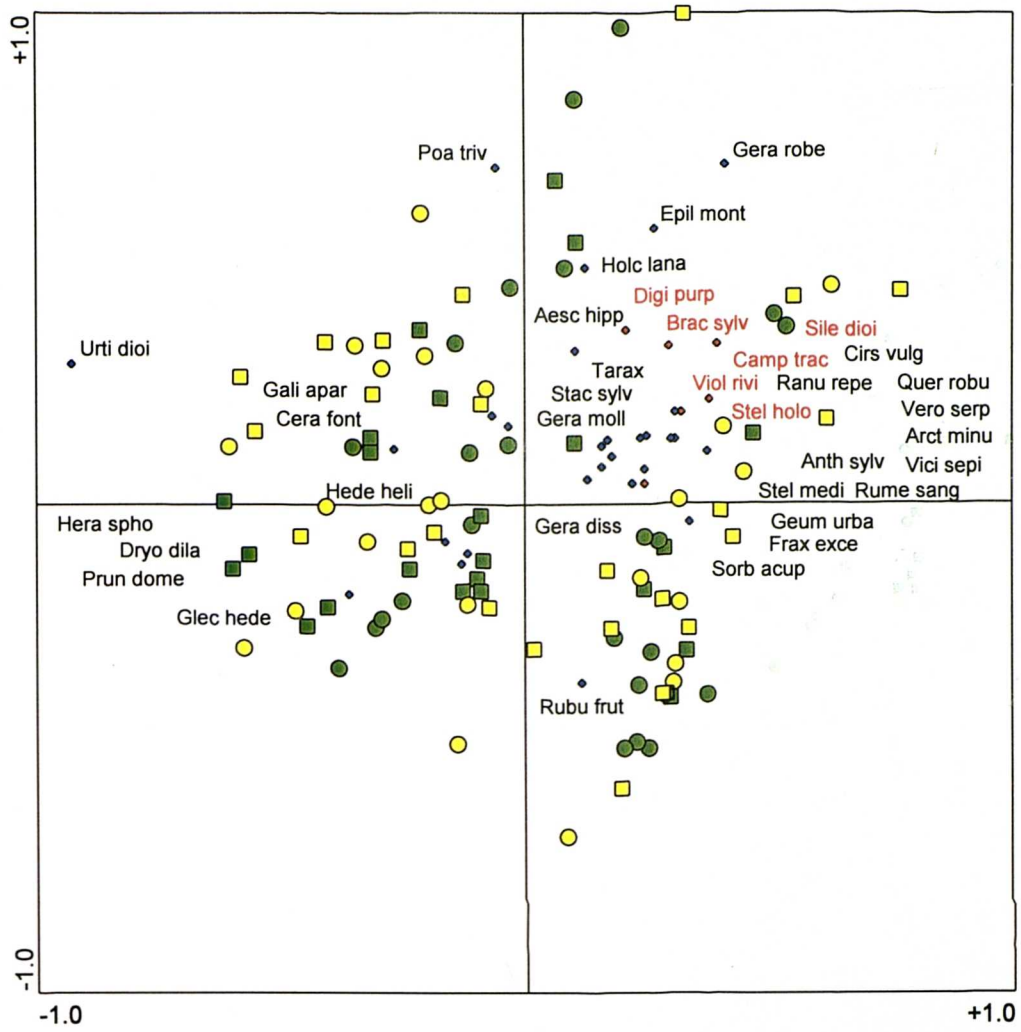


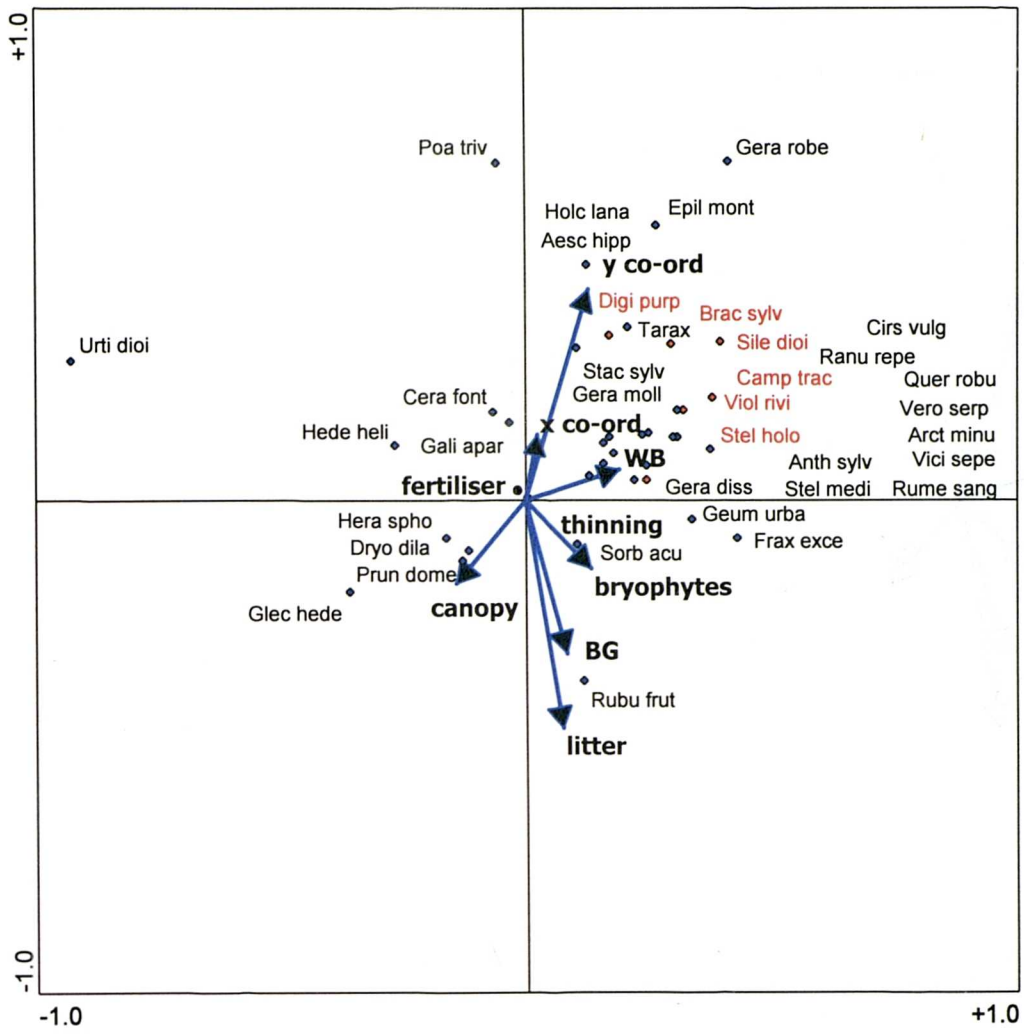
Figure 4.17 Location map of samples recorded in 1999 assigned to TWINSPAN end groups. Treatment plot locations are shown.



Key

- Spontaneous species
- Introduced species
- Samples coded according to treatment:
- Thinned and Fertilised
- Thinned and Unfertilised
- Unthinned and Fertilised
- Unthinned and Unfertilised

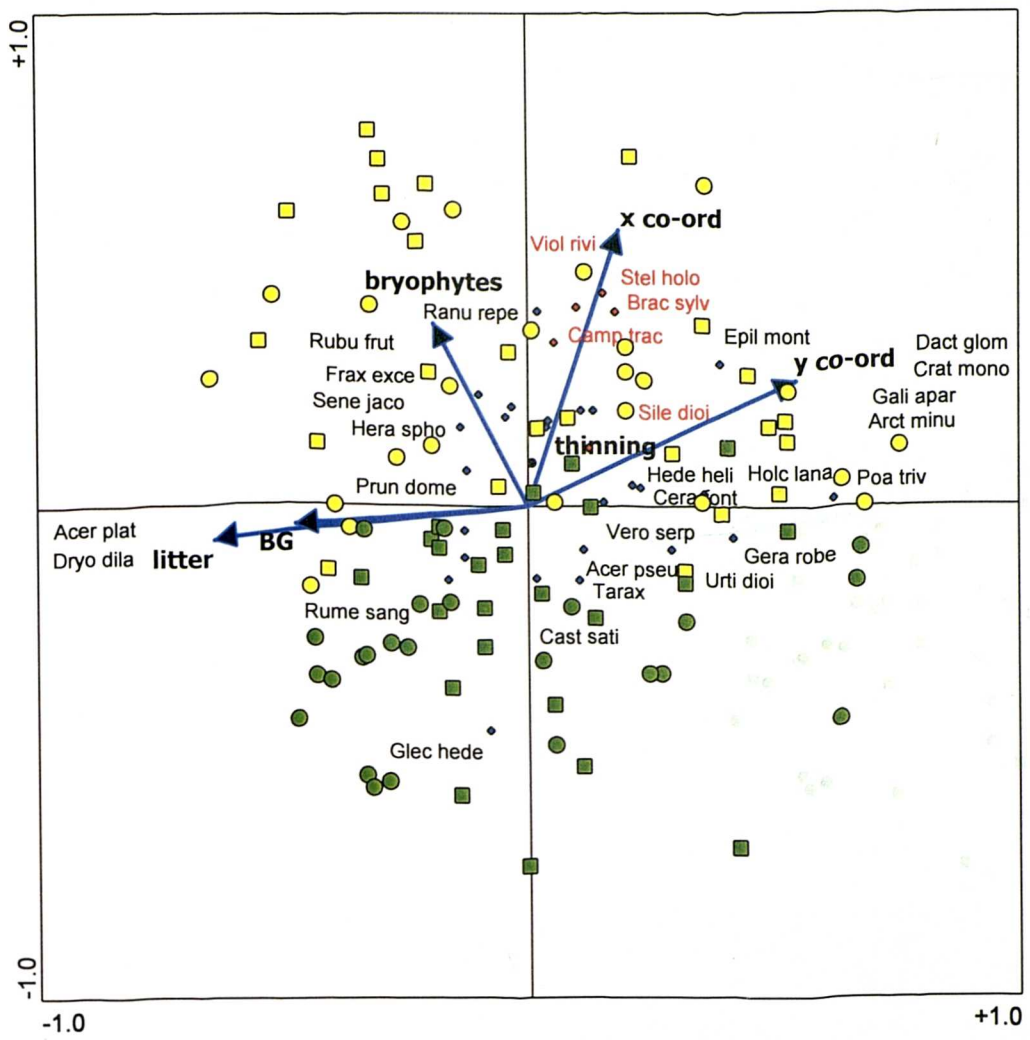
Figure 4.18 Species and sample scatter plot of the first two axes from PCA on the 1998 Nedge Hill vegetation data. This shows the distribution of the vegetation relative to treatment and sample position. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished. Sample numbers are not shown for reasons of clarity.



Key

◆	Spontaneous species	**BG**	Bare Ground
◆	Introduced species	**WB**	Woody Brash
→	Environmental variable	**x co-ord**	x co-ordinate
●	Nominal environmental variable	**y co-ord**	y co-ordinate

Figure 4.19 Species scatter plot of the first two axes from PCA on the 1998 Nedge Hill vegetation data on to which passive environmental variables have been superimposed. This shows the distribution of the vegetation relative to the environmental variables. Introduced and spontaneous species are distinguished.



Key

◆	Spontaneous species	**BG**	Bare Ground
◆	Introduced species	**x co-ord**	x co-ordinate
→	Environmental variable	**y co-ord**	y co-ordinate
•	Nominal environmental variable		

Samples coded according to treatment:

- Thinned and Fertilised
- Thinned and Unfertilised
- Unthinned and Fertilised
- Unthinned and Unfertilised

Figure 4.20 RDA Triplot of species, samples and significant environmental variables for the 1998 Nedge Hill vegetation data. This shows the environmental variables which have a significant relationship with vegetation development. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished. Sample numbers are not shown for reasons of clarity.

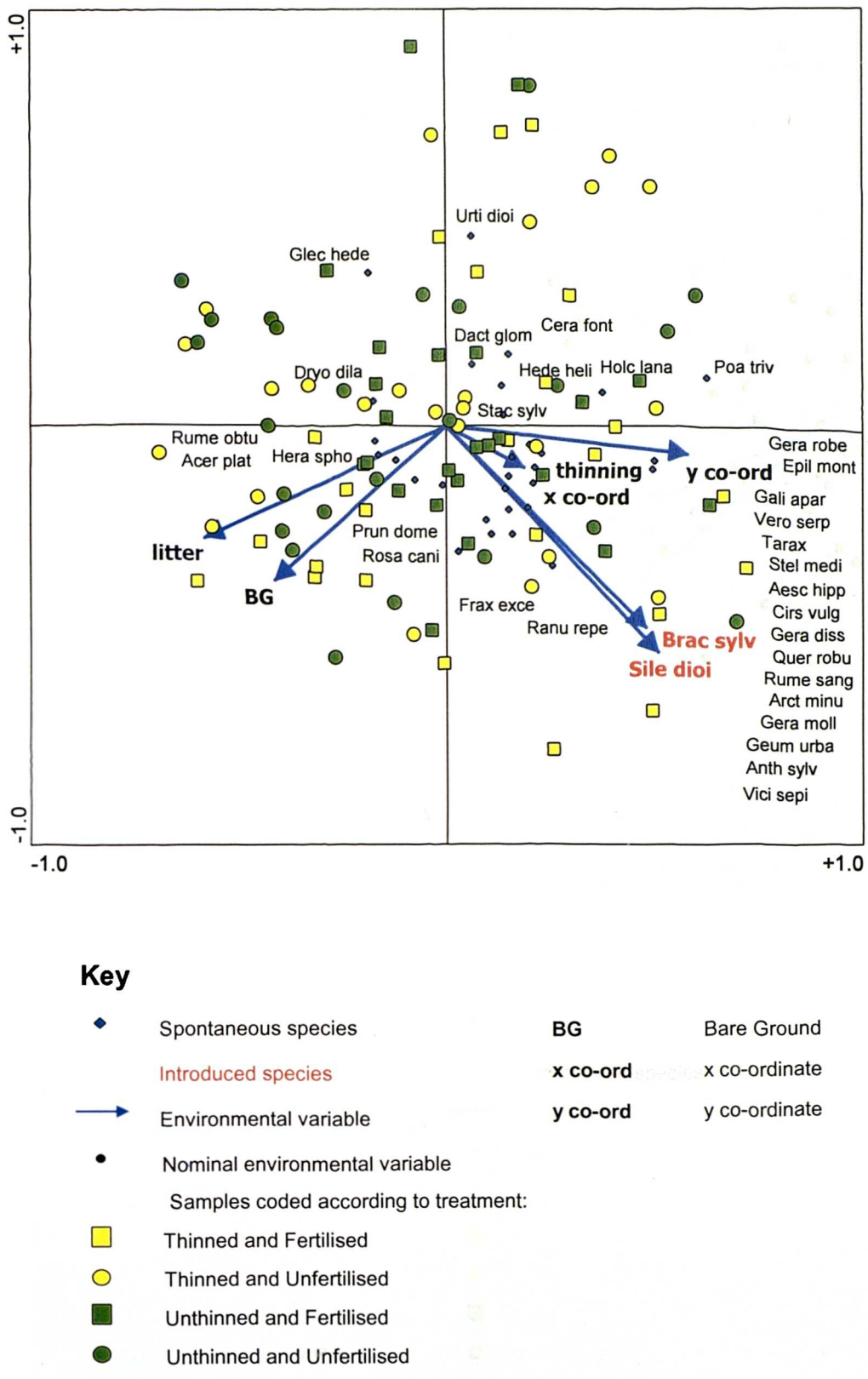


Figure 4.21 RDA Triplot of species, samples and significant environmental variables for the 1998 Nedge Hill spontaneous vegetation data. This shows the environmental variables, including introduced species, which have a significant relationship with vegetation development. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished. Sample numbers are not shown for reasons of clarity. (NB. The species in the bottom right quadrant form a cloud close to the origin).

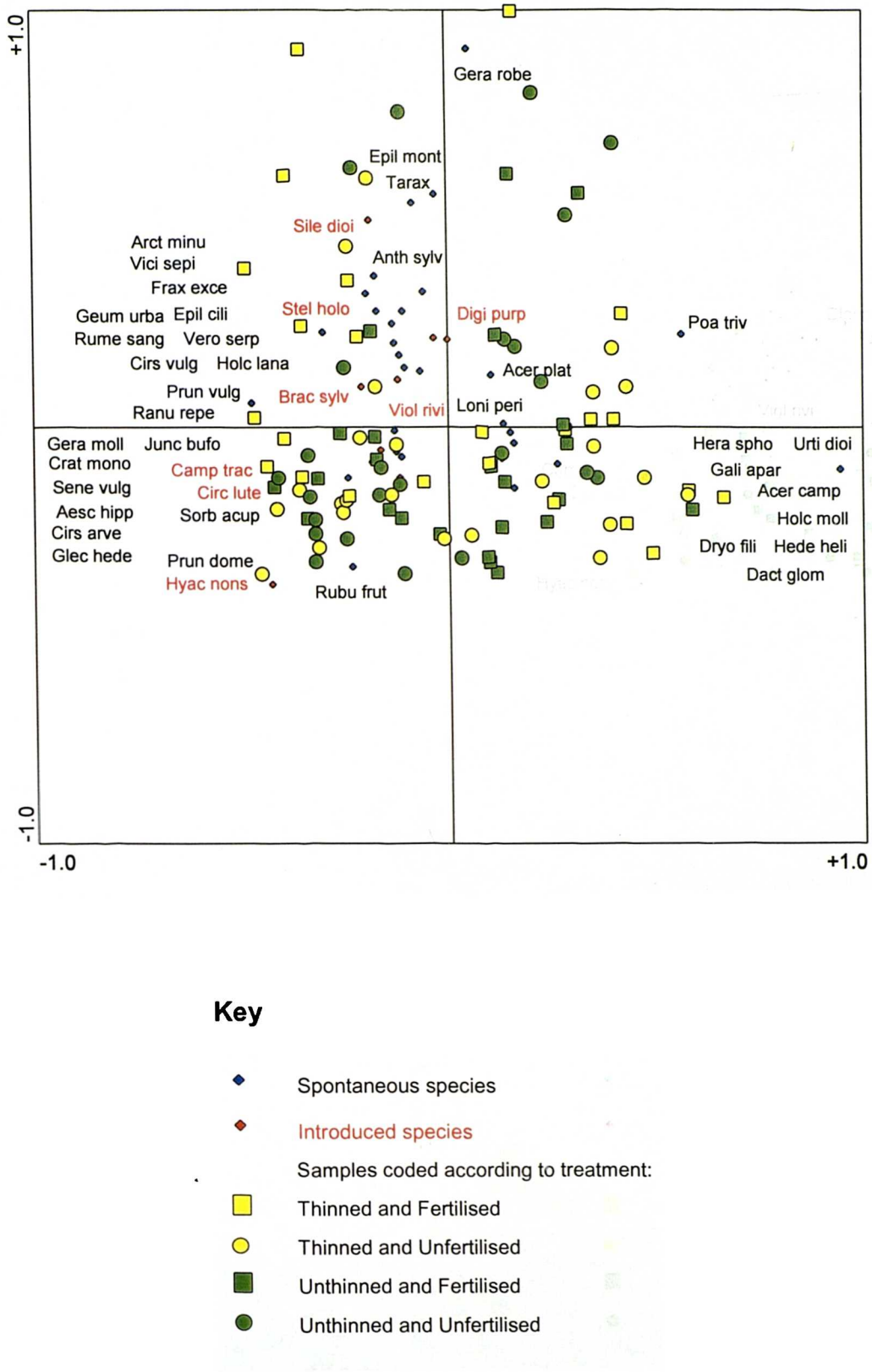
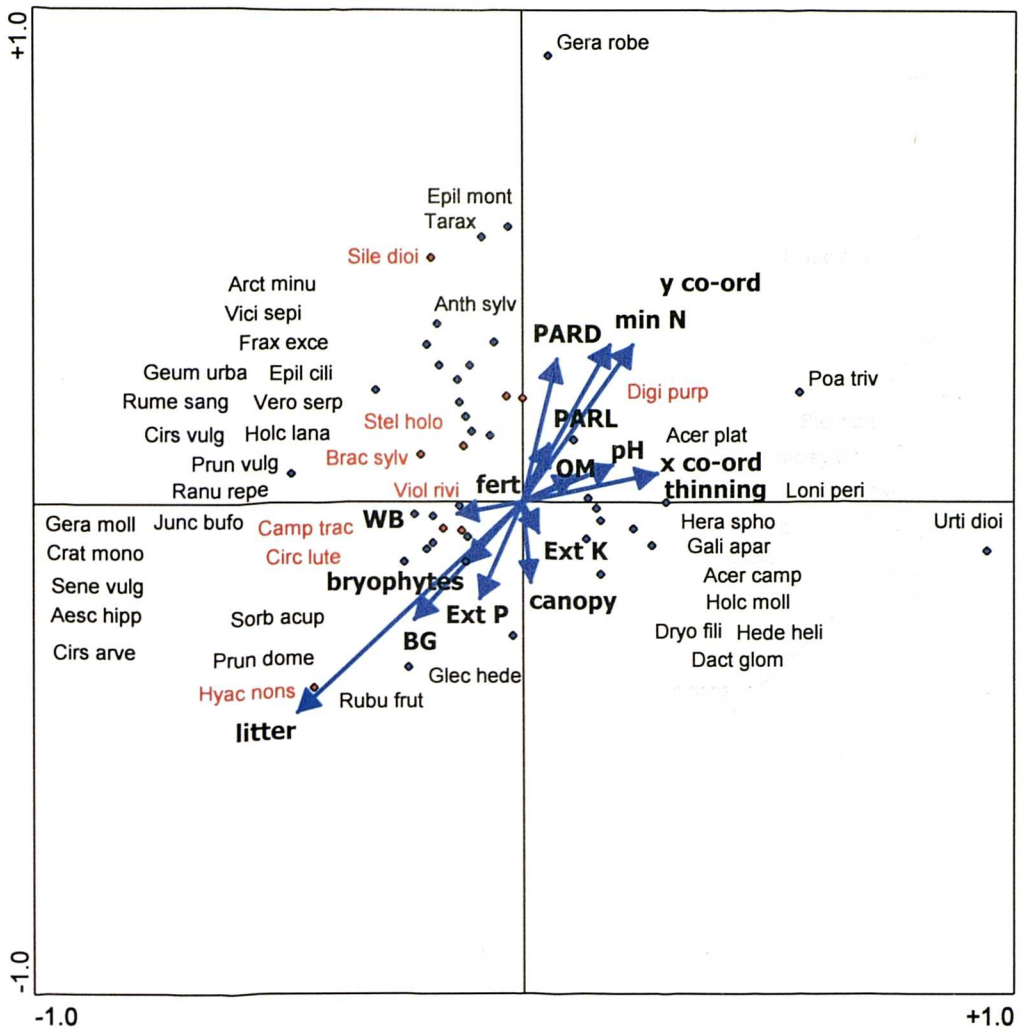


Figure 4.22 Species and sample scatter plot of the first two axes from PCA on the 1999 Nedge Hill vegetation data. This shows the distribution of the vegetation relative to treatment and sample position. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished. Sample numbers are not shown for reasons of clarity.



Key

- Spontaneous species
- Introduced species
- Environmental variable
- Nominal environmental variable

BG	Bare Ground
WB	Woody Brash
OM	Soil organic matter
x co-ord	x co-ordinate
y co-ord	y co-ordinate

Figure 4.23 Species scatter plot of the first two axes from PCA on the 1999 Nedge Hill vegetation data onto which passive environmental variables have been superimposed. This shows the distribution of the vegetation relative to the environmental variables. Introduced and spontaneous species are distinguished.

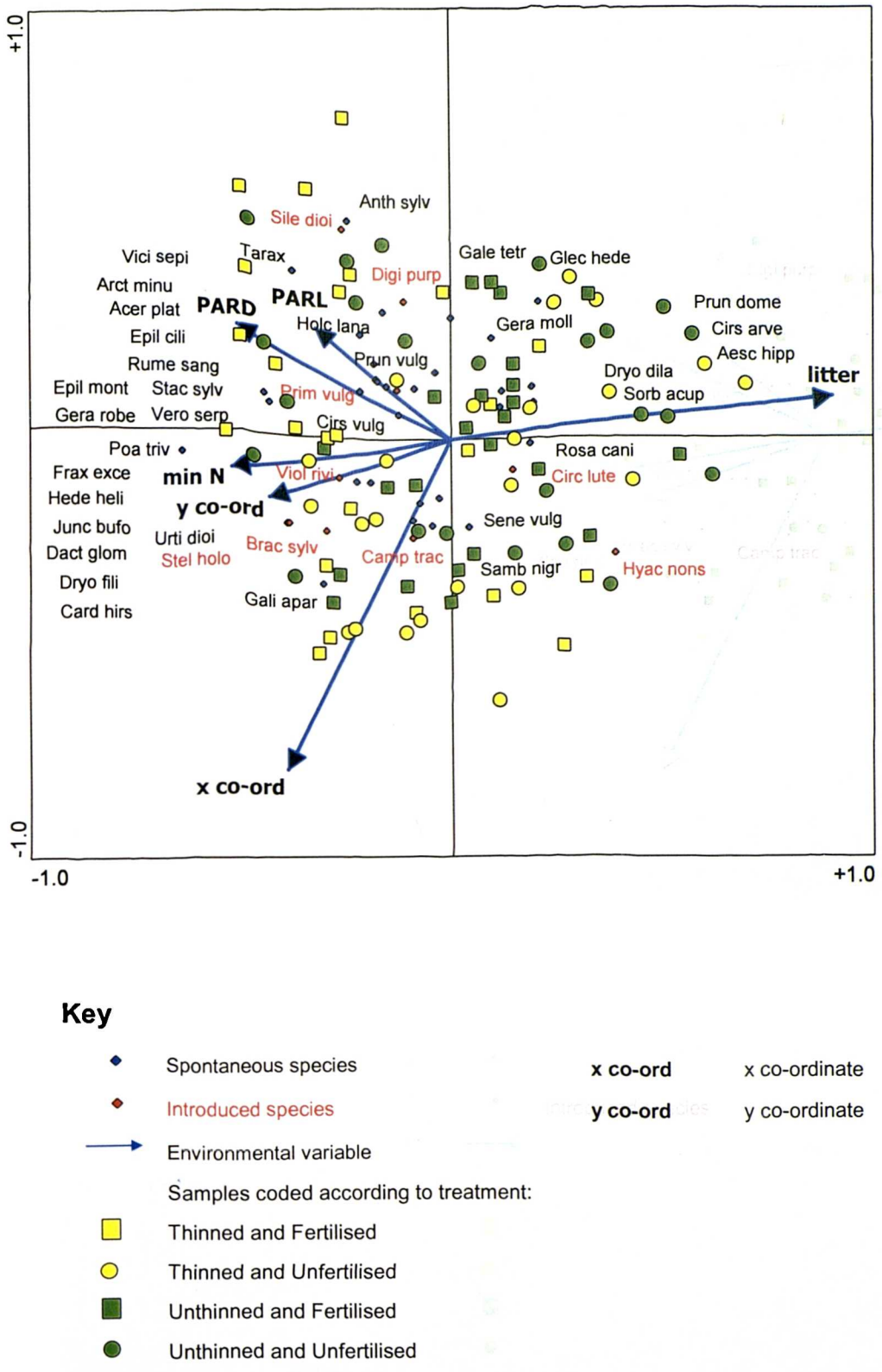
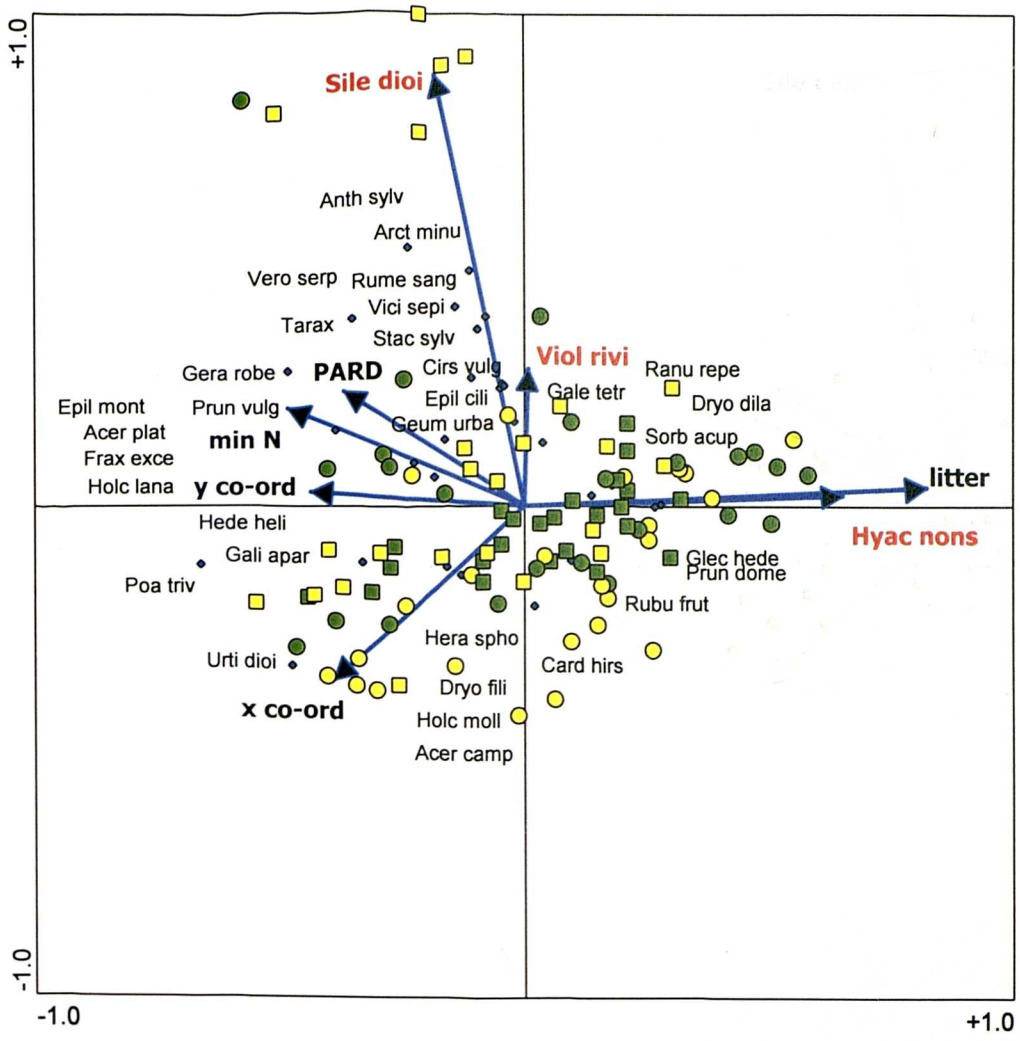


Figure 4.24 RDA Triplot of species, samples and significant environmental variables for the 1999 Nedge Hill vegetation data. This shows the environmental variables which have a significant relationship with vegetation development. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished. Sample numbers are not shown for reasons of clarity.



Key

◆	Spontaneous species	**x co-ord**	x co-ordinate
◆	Introduced species	**y co-ord**	y co-ordinate
→	Environmental variable		
	Samples coded according to treatment:		
□	Thinned and Fertilised		
○	Thinned and Unfertilised		
■	Unthinned and Fertilised		
●	Unthinned and Unfertilised		

Figure 4.25 RDA Triplot of species, samples and significant environmental variables for the 1999 Nedge Hill spontaneous vegetation data. This shows the environmental variables, including introduced species, which have a significant relationship with vegetation development. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished. Sample numbers are not shown for reasons of clarity.

Figure 4.26 Effect of light treatment on mean densities of introduced species occurring in 1998 in Experiment 2. Letters denote statistical difference between means ($p < 0.05$).

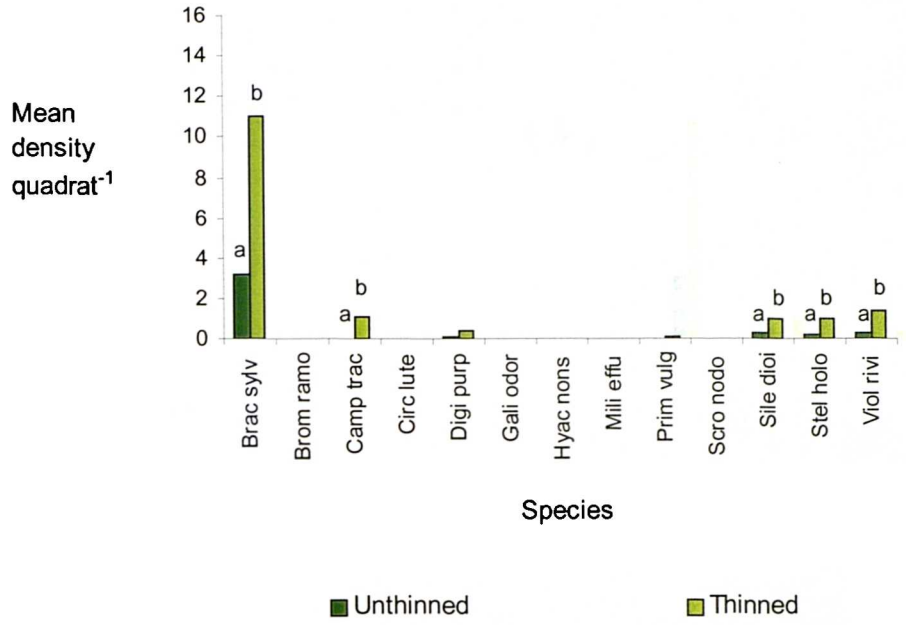


Figure 4.27 Effect of fertility treatment on mean densities of introduced species occurring in 1998 in Experiment 2. Letters denote statistical difference between means ($p < 0.05$).

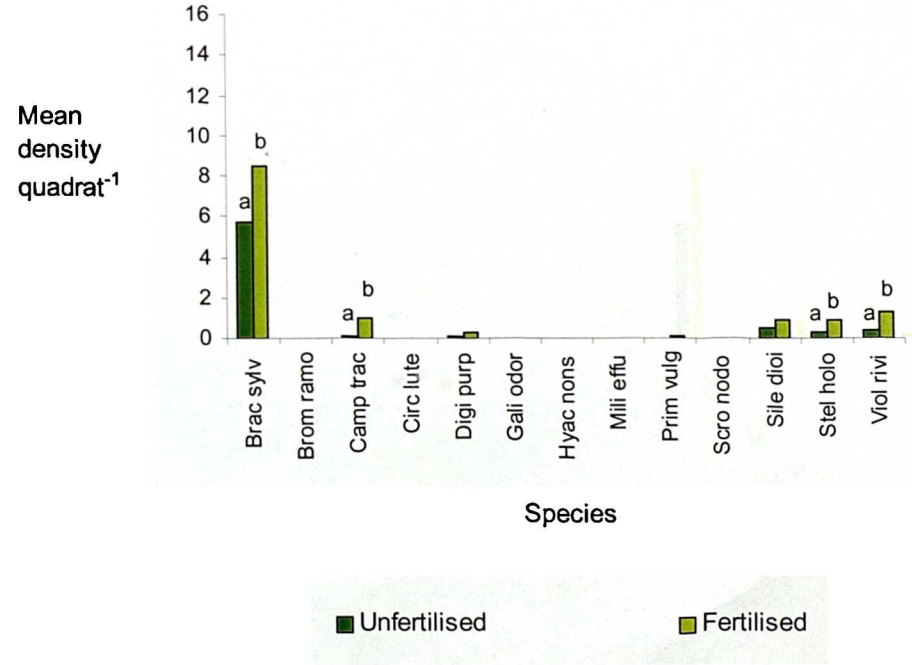


Figure 4.28 Effect of light treatment on mean densities of introduced species occurring in 1999 in Experiment 2. Letters denote statistical difference between means ($p < 0.05$).

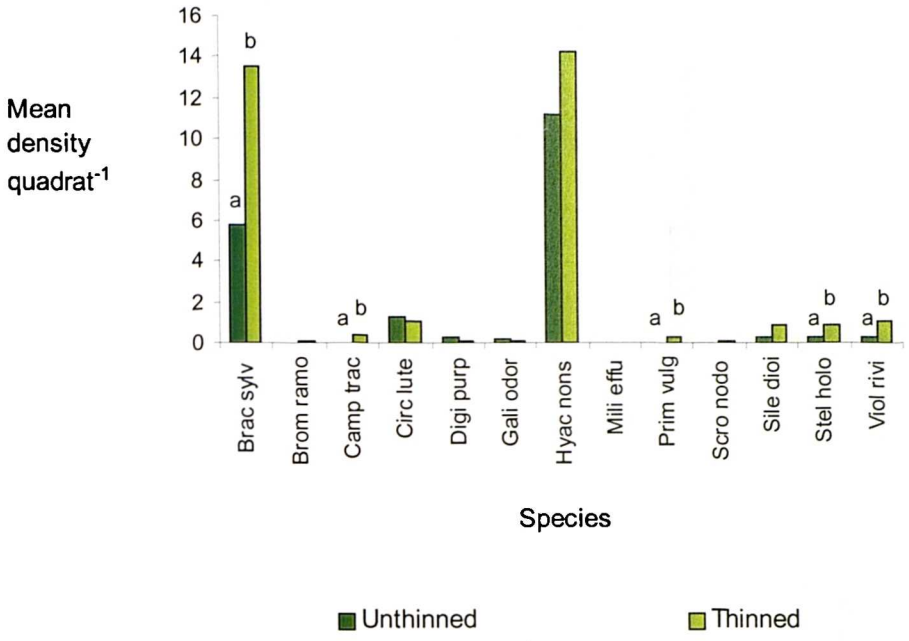


Figure 4.29 Effect of fertility treatment on mean densities of introduced species occurring in 1999 in Experiment 2. Letters denote statistical difference between means ($p < 0.05$).

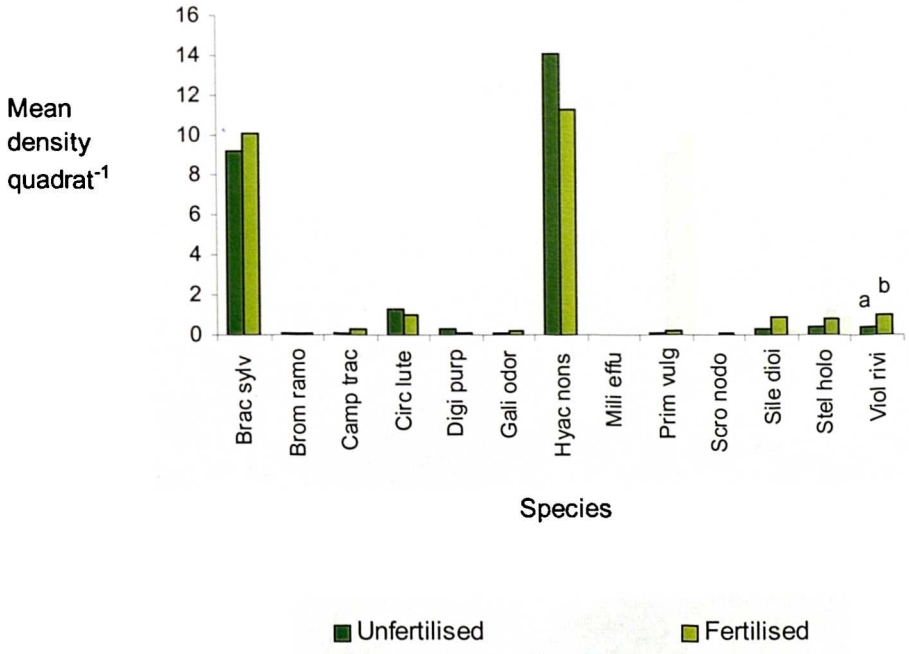
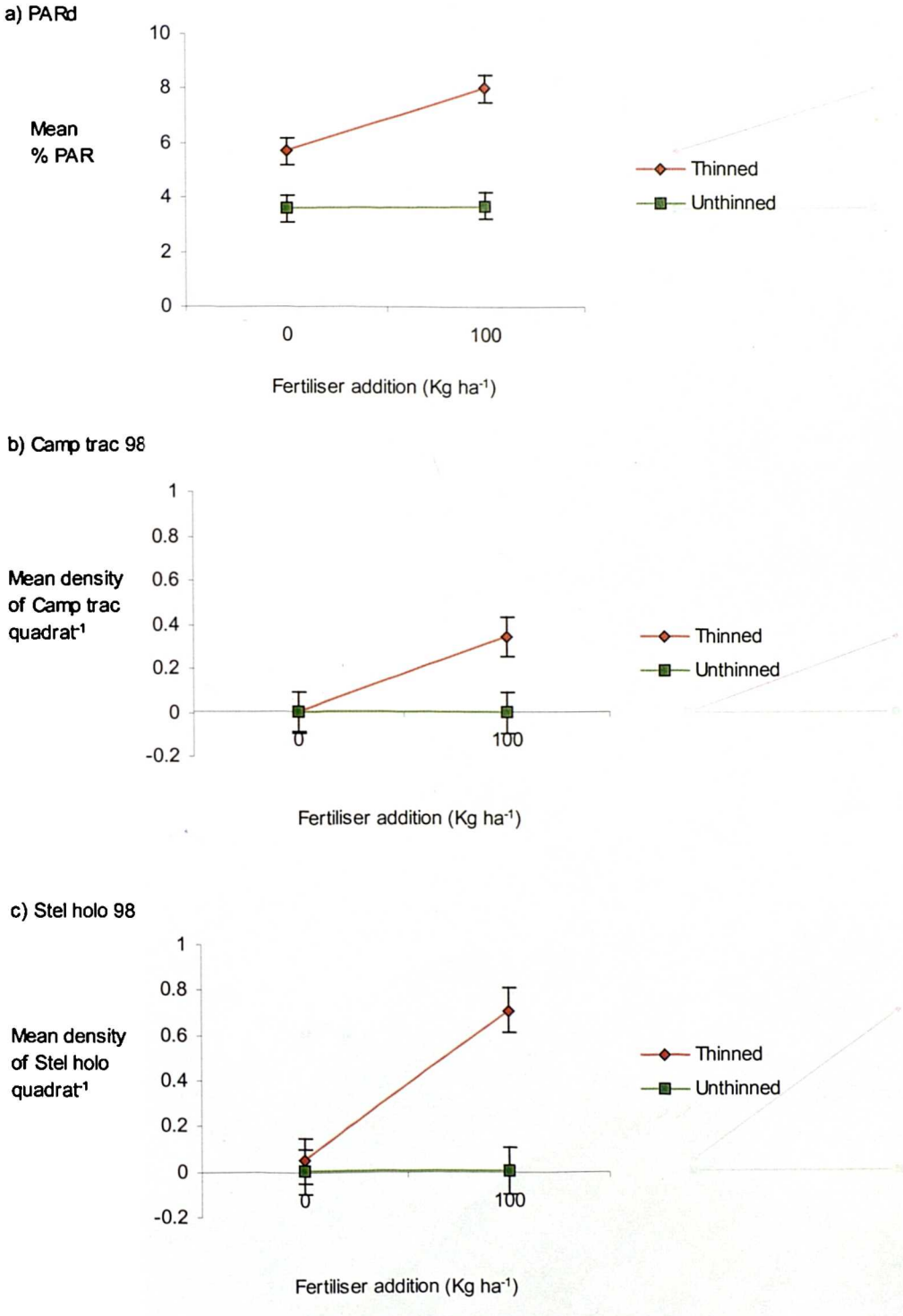


Figure 4.30 Significant interactions ($p < 0.05$) between light intensity and soil fertility treatments on: a) the mean % PAR reaching the woodland floor during the woodland dark phase, and the mean density of introduced species in 1998: b) *Campanula trachelium* and: c) *Stellaria holostea*. Standard error bars are shown.



Chapter 5: Soil Fertility and Light Manipulation Experiments: Experiment 3: Experimental Ground Flora Communities in the Polytunnel at the Plant Environment Research Unit

5.1 Introduction

Experiment 3, the Soil Fertility and Light Manipulation Experiment, carried out at the Plant and Environment Research Unit, Compton, was designed to complement and be compatible with field Experiments 1 and 2 (Section 2.1). This experiment is designed to provide detailed information on the interaction between light and soil fertility within a controlled environment, where experimental design allows elimination of most other environmental variables. Whereas most work to date on the interaction between light intensity and soil fertility, carried out within controlled environments, has been autecological (e.g. Peace and Grubb, 1982), the present experiment is designed to bridge the gap between autecological studies of artificial systems and field experiments.

The experiment aimed to create, within the controlled environment of the polytunnel, artificial ground flora communities that were functionally representative of those created in the field experiments. The aim was to subject these communities to controlled levels of light and soil fertility in a multi-factorial experiment, where species germination, establishment and community development were monitored at regular intervals throughout the 16 month experiment. Harvest of above-ground biomass at the end of the experiment aimed to provide additional information to vegetation survey alone. Experiment 3 was designed to complement the longer-term field experiments, where destructive harvesting was not practicable or desirable.

5.1.1 Aims and objectives

The central aims of Experiment 3: The 'Soil Fertility and Light Manipulation Experiment' in the polytunnel were to:

- Test the hypothesis that in combination and in interaction, soil fertility and light intensity are major determinants of vegetation development in artificial ground flora communities.

- To define the ranges of soil fertility and light intensity which, in combination, optimise vegetation development in the direction of target communities (Section 1.4.1).

The objective of Experiment 3 was to investigate field layer plant communities that develop following experimental establishment within a controlled environment, in relation to variations in soil fertility and light regime, provided by the experimental treatments.

5.2 Methods

5.2.1 Establishment

The experimental ground flora communities were established as follows. The standard seed mix was sown on 21/01/99 (Section 2.3 and Table 2.1) in soil boxes (0.2 m^2 surface area) in the polytunnel at the Plant and Environment Research Unit (Section 2.2.3). Winter sowing was carried out to ensure natural vernalisation of seed. The boxes were straight-sided, rigid, plastic storage boxes measuring 56 cm long, 36 cm wide, 23 cm high, with eight 8 mm drainage holes in the base. The substrate used was compost made up of Compton soil, Ercall soil (Section 2.2.4), peat and grit in a volumetric ratio of 6:1:3:2, respectively; placed on a 3 cm bed of quartzite gravel to aid drainage. Boxes were filled with gravel and compost *in situ* and levelled using wooden supports.

Compton topsoil from abandoned arable land known as the 'barley field' (Section 2.2.3) was employed. McCrea (1999) found this particular topsoil to be suitably nutrient deficient. Soil chemical analyses carried out by ADAS confirmed this to be a very low fertility soil, despite past annual dressings of compound fertiliser. The fact that this was an agricultural soil which had been subjected to frequent herbicide dressings made the potential problem of a large weed seed bank less likely.

Ercall soil was collected from this ancient semi-natural woodland site (Section 2.2.4) in an area marked by an underlying geology of boulder clay and a vegetation conforming to the W8 (*Fraxinus excelsior – Acer campestre – Mercurialis perennis*) target woodland community (Rodwell, 1991). The purpose of adding this woodland topsoil was to inoculate the compost with mycorrhiza, believed by workers such as Fitter (1985) and Francis *et al.* (1986) to play an important functional role in woodland ground flora communities.

Irish moss peat and coarse horticultural grit made up the remaining constituents of the compost, to dilute fertility and aid drainage, respectively. All compost constituents were homogenised in a Pneulac Royer P1 shredder. The homogenised compost was sampled and a full soil analysis was performed by ADAS. Individual boxes of Compton soil, Ercall soil and compost were set up as seed bank trials.

The experimental ground flora communities were subjected to three light treatments and three fertility treatments at low, medium and high levels, provided by horticultural shade netting and N:P:K compound agricultural fertiliser. Each treatment was replicated three times in a multifactorial design (Figure 5.1). Light treatments were randomised within blocks and fertility treatments randomised within the shade treatments in a factorial design.

Various grades of horticultural shade netting (comprising Tildanet tape thread and monofilament netting) were used, singly and in combination, to provide light treatments in the form of tents, supported by purpose built rectangular tubular steel frames. These were placed over the soil boxes to give approximately 30%, 20% and 5% of ambient light levels. The fertility treatments involved top dressing with N:P:K fertiliser at standard field rate (100 kg ha^{-1}) (Section 2.1.2) and at double this amount (200 kg ha^{-1}), in 50 kg ha^{-1} doses, plus a control. Each dose was separated by three weeks, in order to minimise scorching and osmotic shock to seedlings and seeds, respectively, (Section 2.1.2). Fertilisation was carried out on 04/03/99, 25/03/99, 19/04/99 and 10/05/99. Plate 5.1 shows the experiment at establishment. The form and layout of the light treatments (a), fertility treatments and seedbank trials (b) can clearly be seen.

5.2.2 Environmental monitoring

The experiment was maintained by consistently applied surface watering with tap water when required. A fine-rose watering can was used to minimise soil erosion and plant damage. A thermohydrograph was used to continuously monitor the internal environment of the polytunnel with respect to relative air temperature and humidity, for the duration of the experiment. PAR was measured at regular intervals during the growing season, expressing mean sample PAR as a percentage of the average ambient solar radiation outside the polytunnel (Section 2.4). The ambient light intensity within the polytunnel was recorded on each occasion for comparison.

5.2.3 Vegetation survey

It was believed that use of an agricultural soil subjected to frequent herbicide dressings, as the base of the compost would minimise the potential problem of a large weed seed bank. However, the initial community that developed following sowing was an arable weed flora dominated by *Fumaria officinalis,* with abundant *Spergularia arvensis* and *Tripleurospermum inodorum.* Few introduced species were represented in this initial community; *Brachypodium sylvaticum* and *Bromopsis ramosa* occurred most frequently (Section 5.3.1). The seedbank trials demonstrated that it was the Compton soil that was the source of these arable weeds. It was therefore decided, once the fertiliser dressings were complete and the experiment was fully established, to harvest this weed flora in order to reduce its influence on the target vegetation. On 10/05/99 and 11/05/99, all spontaneous species were harvested at ground level and removed from the experiment. The spontaneous above-ground biomass from each box was combined in brown paper bags, weighed and dried to a constant weight in an oven at 80°C for 48 hours. After drying and cooling in a desiccator, samples were then reweighed.

The vegetation was surveyed on five occasions during the 1999 and 2000 growing seasons (Section 2.5). Table 5.1 shows the survey dates and the parameters recorded at each survey. Each survey took about a week to complete. In the periods between survey dates the basic phenology of introduced and key spontaneous species was recorded, including flowering and seeding periods. Regular photographic recording of the experiment was also carried out. Photographs of the vegetation in each sample box were taken shortly after establishment (i.e. at the first signs of germination) and immediately prior to the commencement of each survey.

Table 5.1 Vegetation parameters measured and recording dates for the surveys undertaken in Experiment 3.

Survey	% Cover	Density	Height	Biomass	Recording Dates
1		X			13/04/99–16/04/99
Initial weed harvest				X	10/05/99-11/05/99
2	X	X			03/08/99–06/08/99
3	X	X			06/10/99–11/10/99
4	X		X		28/04/00–29/ 04/00
5		X (introduced)	X (introduced)	X	11/05/00–22/05/00

In surveys 1–3 the densities of all vascular plant species were recorded. In survey 1, recorded just prior to the weed harvest, density only was recorded, as percentage cover was difficult to determine in the dense matrix of weed seedlings. Survey 4 represents the vegetation survey immediately prior to the biomass harvest of survey 5. Densities of introduced species were determined at harvest. It was judged too difficult, at harvest, to separate individuals of many of the spontaneously occurring species, especially the grasses. Densities of introduced and spontaneous species were summed per sample, where data were available. The percentage cover of all vascular plant species was recorded in surveys 2–4. The mean heights (cm) of all vascular plant species and introduced species were recorded in surveys 4 and 5, respectively.

During the survey 5 harvest, all vascular plants were cut at ground level, sorted by species, placed into brown paper bags, and fresh- and dry-weighed, as described above for the initial weed harvest. The resulting weights were summed per sample to calculate the fresh and dry weights of the introduced species, the spontaneous species and the total biomass response. The harvest was timed to coincide with maximum community development and minimum die back of the dominant biennial *Silene dioica*. Many workers (e.g. Wijesinghe and Hutchings, 1999) have commented on the relative importance of both root and shoot resource allocation when carrying out biomass studies. At the outset of this experiment it was the intention to harvest the below-ground biomass of at least the introduced species, however in practice, this proved too difficult to carry out with sufficient accuracy to give useful results.

As either *Silene dioica* or *Scrophularia nodosa* came to dominate the experimental communities during the latter stages of the experiment, these two species were selected for extra scrutiny. During the harvest in survey 5, three representative stems of these species were taken from each box and measured individually for: stem length (cm), leaf area (cm^2), leaf and stem fresh and dry weights (g).

5.2.4 Soil survey and analysis

During the biomass harvest, soil sampling was carried out immediately after the above-ground biomass had been removed from each box (Table 5.1). Five trowel samples from the centre and corners (avoiding the edges) of each box were bulked to form a single sample for each box. Soil samples were prepared and stored as described in Section 2.6.1. The timing of soil sampling to coincide with maximum nutrient uptake by field layer plants mirrors that carried out in the field experiments (Section 2.6.1). Chemical analyses were conducted to quantify indicators of soil fertility. Soil pH and mineralisable nitrogen, extractable phosphorus and potassium, plus percentage soil organic matter were measured, as described in Sections 2.6.2-2.6.6, respectively.

5.2.5 Statistical analysis

5.2.5.1 Environmental variables

ANOVA were performed on all environmental variables, including 'vegetation environmental variables' and vegetation response measures (Sections 5.2.5.2-5.2.5.4) to investigate between-block variation and treatment effects (Section 2.7.1.2). The ANOVA were set up using the factorial design as a two-way ANOVA (in randomised blocks). Light treatments were randomised within blocks, and fertility treatments randomised within light treatments (Figure 5.1). Treatment significant results are presented in ANOVA tables and tables of treatment means, with the exception of the vegetation response measures, whose treatment means are presented in bar charts (Sections 5.2.5.3 and 5.2.5.4). Significant interactions between the light and fertility treatments (where both main effects were also significant) are presented as line graphs.

5.2.5.2 Vegetation and environmental data

Vegetation data and environmental variables representing soil fertility (Section 5.2.4) and the light climate (Section 5.2.2.) plus 'vegetation environmental variables', were examined in CANOCO, to determine the environmental influences on the establishment of introduced species and on the direction of vegetation development (Section 2.7.2.2). As the soil

fertility variables were measured at the end of the experiment, they were only included in the analysis of survey 4 vegetation data. Interactions between significant variables were also investigated. In order to elucidate more subtle underlying influences on the vegetation, partial direct gradient analysis was also used to remove variation from the model due to certain significant environmental variables (by treating them as covariables). PCA results are presented in scatter plots, some with all environmental variables passively superimposed, to illustrate their relative effects, and RDA results are presented in biplots and triplots (Section 2.7.2.2).

5.2.5.3 Biomass and height data

Biomass data (dry weight) was used to create a species abundance table for the three light treatments. The rationale behind using biomass data, as opposed to presence / absence vegetation data, was to produce a more precise picture of the different plant communities that developed under the three light treatments. The NVC constancy tables (Rodwell, 1991) were used as a model. The dry weight of each species was averaged across light treatments. These means were then used to calculate the percentage contribution that each species made to the total plant biomass under each light treatment. These percentages were then transformed using a base 10 logarithm. This log scale was then evenly divided to produce five abundance classes. Species that contributed less than 3 g dry weight to the overall biomass and / or occurred in three quadrats or less (the size of a single replicate) were disregarded. ANOVA were carried out on the biomass and height variables (Sections 5.2.3 and 5.2.5.1), to investigate treatment differences in terms of plant production and stature as well as in community composition (Section 2.7.3.2).

5.2.5.4 Species density and recruitment data

ANOVA were performed on introduced and spontaneous species density data (Σx) (Section 5.2.3) to examine treatment effects (Section 2.7.3.2). Recruitment levels of introduced species were calculated between surveys (Section 5.2.3) and were also subjected to ANOVA to investigate treatment effects on recruitment. Densities of individual introduced plant species were also investigated in this way (Section 5.2.3). Any plot position effects were identified here and potential causes investigated (Section 2.7.3.2).

5.3 Results

5.3.1 Physiognomy

Plate 5.2 illustrates (via a typical sample box) the sequential development of the experimental ground flora communities, from initial germination (a) and early development of the arable weed flora dominated by *Fumaria officinalis* (b), through to establishment of the post weed harvest ground flora communities (c) and their maximum development (d).

The photomontage in Plate 5.3 shows a typical replicate of the experiment at the stage when the post-weed harvest ground flora communities have become well established. The major visual difference between the light treatments is illustrated by the domination of the plant communities by *Siliene dioica* in the two higher light treatments and by *Scrophularia nodosa* in the lowest light treatment. Differences in biomass, plant stature and etiolation between the light treatments were also evident. Plant biomass and stature successively increased in the higher light treatments. However, etiolation of plants subjected to the lowest light treatment, produced relatively tall plants with much reduced biomass.

Visual differentiation between the fertility treatments was less obvious. However, these differences due to treatment were discernible under the two higher light treatments. The colour, biomass and height of the vegetation appeared to change with fertility treatment. The controls can be clearly distinguished from the other fertility treatments by their low growing yellowish-green vegetation. Vegetation growing in fertilised sample boxes appeared to be larger, lusher and greener, with biomass, height and colour intensity apparently increasing with fertility. However, these observed differences between the two fertilised treatments were not clear across the whole experiment and occasionally appeared reversed.

5.3.2 Environmental variables

5.3.2.1 Light climate

The results of ANOVA on the measured light climate variable, PAR, are shown in the ANOVA table (Table 5.2) and table of means (Table 5.3). Results were almost identical, regardless of when the light climate was monitored, although all light climate monitoring was done under specified conditions (Section 2.4). Light treatment had a highly significant effect on light climate (Table 5.2), with PAR infiltration levels matching closely the levels predicted for each light treatment, i.e. 5%, 20% and 30% PAR infiltration (Table 5.3). Table 5.2 shows that this result is not complicated by any affects of fertility treatment or

plot position, i.e. block effects. The CANOCO analyses (Section 5.3.3) provide further evidence of the effect of light treatment on light climate.

5.3.2.2 Soil environment

Significant ANOVA results on the soil variables are shown in the ANOVA table (Table 5.2) and means are presented in Table 5.3. Spatial variation in mineralisable nitrogen was not effected by either light or fertility treatment, or block position. As the experiment was designed to minimise background variation in soil variables it is assumed that mineralisable nitrogen has a fairly uniform spatial distribution. CANOCO analyses (Section 5.3.3) were used to investigate any influence on vegetation development.

The remaining measured soil variables, extractable potassium and phosphorus, pH and soil organic matter, were all affected by experimental treatment, but not block position (Table 5.2). Extractable potassium, extractable phosphorus and pH were all influenced by fertility treatment (Table 5.2). As expected, extractable potassium and phosphorus concentrations increased with successively higher levels of fertilisation, and pH levels declined with increasing fertilisation (Table 5.3). The effects of N:P:K fertiliser additions, by way of increased concentrations of extractable potassium and phosphorus and soil acidification, were detectable a year after application. However, extractable potassium and phosphorus were both affected as much (and more so in the case of potassium) by light treatment as they were by fertility treatment (Table 5.2). Both extractable potassium and phosphorus concentrations were much greater under the lowest light treatment (5% PAR transmission), with potassium showing higher concentrations under the highest light treatment (30% PAR), compared to the medium light treatment (20% PAR) (Table 5.3). This evidence suggests that potassium uptake by the artificial ground flora communities was maximised under the medium light treatment (20% PAR), and that uptake of both potassium and phosphorus was severely limited under the lowest light treatment (5% PAR).

This evidence demonstrates the huge impact that light intensity can have on nutrient uptake by ground flora plants, although no interaction was detected between light and fertility treatments on any of the soil variables (Table 5.2). Soil organic matter was significantly influenced by light treatment (Table 5.2), with the greatest percentage soil organic matter occurring under the lowest light treatment (5% PAR) and the smallest percentage under the medium light treatment (20% PAR) (Table 5.3). This perhaps indicates inefficient humification of organic matter due to darker and therefore colder conditions under the 5%

PAR light treatment, or possibly a greater source of organic matter, as certain plants experience die back due to light stress. The most efficient use of organic and mineral soil resources appears to occur under the medium light treatment.

5.3.3 Vegetation and environmental data

The vegetation response recorded immediately prior to the final biomass harvest (i.e. survey 4) is the main focus of the multivariate analyses, as this is taken to represent the complete response of plant community development. This response can be analysed in conjunction with the measured soil and light parameters. The pre-harvest plant communities, recorded in survey 4 (Plate 5.2 (d)), comprised a mixture of introduced woodland species, which tended to dominate the composition and structure of the vegetation, and spontaneous species consisting predominantly of arable weeds with a few woodland species, arising from the ancient woodland soil component of the compost. Vegetation parameters, such as litter, bare ground, woody brash and bryophyte cover, which were investigated in the field experiments as potential environmental influences on vegetation development, were largely absent from the artificial communities in the polytunnel. The percentage cover of bryophytes and algae were recorded, but they were not present in sufficient quantities to justify inclusion in the statistical analyses.

Ordination analyses were used to identify axes of variation, or environmental gradients, affecting vegetation development. The ordination diagrams (Figures 5.2–5.8) were created and presented as described in Section 2.7.2.2. Sample numbers are given, and samples may be located within the experiment by referring to Figure 5.1. The scatter plot in Figure 5.2 illustrates the relative positions of both species and samples under a PCA analysis performed on the pre-harvest (i.e. survey 4) vegetation data. ANOVA analyses of the sample ordination scores for the first two axes of variation show that light treatment had a significant effect on axis 1 scores (Table 5.2). *Post-hoc* tests revealed that the lowest light treatment was significantly different from the two higher light treatments (Table 5.3). Fertility treatment had no effect on axis 1 sample scores (Table 5.2). No treatment effects were identified on ordination scores for the second axis of variation produced by the PCA (Table 5.2). This evidence indicates that light intensity, as influenced by light treatment (Section 5.3.2.1), has a major effect on the vegetation, creating distinctly different communities under the lowest light treatment (5% PAR transmission). No fertility effect, on the entire vegetation, was detectable using ANOVA.

PCA analysis of the pre-harvest vegetation data, suggests that the two most important axes of variation in the data represent light and soil fertility, respectively (Figure 5.2). The evidence that supports axis 1 (the horizontal axis) as representing light climate is: the polarisation along axis 1 between the shade-tolerant introduced (and spontaneously-occurring) woodland species and the light-demanding arable weeds. *Silene dioica* is the major exception to this trend, occurring at the extreme light end of this axis. *Silene dioica* is a hedgerow species, and although it is tolerant of more than moderate shade levels, it responds positively to increased light intensity, when available (Willmot and Moore, 1973). The introductions *Stellaria holostea* and *Viola riviniana,* and the spontaneous woodland species *Anemone nemorosa*, are centrally distributed on the 'light axis'. *Stellaria holostea* is a resource-demanding hedgerow species (Lawley, 1998), whereas, *Anemone nemorosa* is a woodland herb which evades shade via its vernal phenology and *Viola riviniana* is shade-tolerant, but can thrive in open habitats (Grime *et al.*, 1998). The introduced species *Silene dioica* and *Scrophularia nodosa* are polarised at opposite ends of axis 1. *Silene dioica* dominates the plant communities that were subjected to the two higher light regimes, whereas, *Scrophularia nodosa* is the dominant species under the lowest light treatment (Plate 5.3). The sample distribution along axis 1 clearly supports the idea that this is a light axis with light intensity increasing towards the left-hand side of the scatter plot (Figure 5.2). The significant effect which light treatment had on axis 1 scores in the ANOVA of the PCA sample ordination scores adds statistical weight to the interpretation of axis 1 as a light gradient (Tables 5.2 and 5.3).

No treatment effects were identified on ordination scores for the second axis of variation (Table 5.2). There is, however, some evidence that axis 2 represents a fertility gradient. The distribution of species and samples along axis 2 of Figure 5.2 is less well defined than that of axis 1. Most species and samples are aggregated around the centre of the axis. However, those that do deviate from this pattern in the upper half of the scatter plot, represent nutrient-demanding species and samples, which were subjected to higher levels of fertilisation. Lawley (1998) found that *Stellaria holostea* was preferentially associated with higher soil fertility levels. This species appeared throughout the experiment as seedlings or small trailing plants, but in places it formed large spreading patches, which tended to occur in one of the two fertilised treatments.

Figure 5.3 shows the same PCA results as Figure 5.2, but with all environmental variables passively superimposed onto the species scatter plot. The position of both the ordinal light treatment variable and measured PAR vectors, adds weight to the assumption that axis 1 represents light intensity, and supports the use of measured PAR to represent light treatment. The ordinal fertility treatment variable is most closely associated with axis 2, supporting the PCA evidence that axis 2 represents a fertility gradient. Mineralisable nitrogen is most closely associated with the fertility treatment variable, perhaps suggesting that it is the nitrogen aspect of fertility that has the greatest influence linked with fertilisation. However, ANOVA have shown that fertility treatment had no effect on mineralisable nitrogen (Section 5.3.2.2). The soil variables extractable potassium and organic matter are also associated with axis 1 of the PCA (Figure 5.3), but act in the opposite direction to the light variables, with higher concentrations of potassium and percentages of soil organic matter associated with lower irradiance. Extractable phosphorus appears to act in a similar plane to extractable potassium, but is less significant and has no obvious correlation with either axis of variation. This evidence supports the relationship, found under ANOVA, between light treatment and extractable potassium and phosphorus, which was more significant, in the case of potassium, than the increased concentrations afforded by fertility treatment (Section 5.3.2.2). Soil pH was more allied to axis 1 and opposed soil organic matter, the accumulation of which would acidify the soil surface layers. This evidence suggests that light intensity and soil fertility are major determinants of vegetation development in artificial ground flora communities. Direct ordination analyses were used to further investigate this assertion.

The interpretation of the two most important axes of variation occurring in the data as representing light and fertility, respectively, is supported by the direct gradient analyses of the RDA model, shown in the triplot (Figure 5.4). The triplot shows that light intensity (as measured by PAR) and fertility (represented by the ordinal treatment variable), respectively, represent the first two axes of variation within the vegetation data, and significantly influenced vegetation development.

On comparison of the indirect (PCA) and direct (RDA) gradient analyses (Figures 5.2 and 5.4, respectively), it can be seen that the introduced species, apart from *Silene dioica,* are negatively associated with PAR. The major difference between the above two analyses is that both axes have 'flipped over', so that light increases from left to right and fertility from top to bottom in the RDA triplot of Figure 5.4. The spread, of species and samples, along

the fertility axis is more marked under direct gradient analysis. Here the introduced grasses, *Brachypodium sylvaticum, Bromopsis ramosa* and *Milium effusum,* and the nutrient demanding herb *Stellaria holostea,* are positively associated with fertility. This implies that the introduced grasses were able to take advantage of increased fertility (at lower light levels), and were therefore stronger competitors than the introduced forbs. Cohn (1994) found in autecological studies of *Silene dioica, Circaea lutetiana* and *Viola riviniana* that these species did respond positively to increased levels of fertility. However, in the present experiment, at lower light intensities *Circaea lutetiana* and *Viola riviniana* were unable to take advantage of the highest level of fertility, because of competition with the woodland grasses. *Circaea lutetiana* and *Viola riviniana* were associated with moderate fertility levels (i.e. 100 kg ha^{-1} addition of N:P:K compound agricultural fertiliser). This pattern does not, however, apply to the spontaneous species, which with the exception of the introduced species *Silene dioica,* dominated communities under higher light regimes. Tall ruderal forbs, such as *Solanum nigrum, Chenopodium album* and *Senecio jacobea* out-competed the spontaneous grasses (which are only associated with moderate fertility) at higher fertility levels.

The sample ordination, shown in the triplot of Figure 5.4 shows clear differentiation between both light and fertility treatments. Samples from treatment replicates form tight clusters, with the exception of those from the high light treatment, which form a looser group with some differentiation on the light axis. The near equidistant positioning of the different treatments in ordination space allows autecological predictions of resource preferences of target species grown in a competitive community environment. For example, *Silene dioica* dominated communities subjected to PAR at > 20% of ambient levels, but was preferentially associated with those communities receiving > 30% PAR and moderate fertiliser additions of 100 kg ha^{-1}. By contrast, *Scrophularia nodosa* (also associated with moderate fertility) was the dominant species in highly shaded communities only receiving about 5% of ambient light levels.

The vegetation response of this experiment indicates that, with the exception of *Silene dioica,* target ground flora species were favoured by light intensity (PAR) in the range 5–20% of ambient levels, and soil fertility augmented by up to 100 kg ha^{-1} addition of N:P:K agricultural fertiliser. Although *Silene dioica* is more shade-tolerant than this experiment suggests, it is thought that the double layer of shade netting, used to make up the lowest light treatment, restricted air flow to such an extent that the initially vigorous *Silene* plants

became infested with mildew and rotted. Grime and Jeffrey (1965) reported how the relationship between irradiance and growth rate is complicated by the vulnerability of shade-intolerant species to fungal attack. Although *Silene* is not shade-intolerant, excessive growth stimulated by shaded conditions can deplete energy reserves, leading to a predisposition to fungal attack (Morgan and Smith, 1979). *Scrophularia* rapidly occupied the empty niche and came to dominate these shade communities.

The significant environmental variables light and fertility appear perpendicular to each other in the ordination space of Figure 5.4. This indicates that these variables were acting independently, rather than in interaction. However, a significant interaction between the light and the fertility treatment factors was found using RDA (Figure 5.5). When the two treatment factors were combined as an interaction, extractable potassium appeared to have a significant influence on the vegetation. Together both treatment factors accounted for 31.4% of the variation in the species data. Figure 5.5 suggests that competitive ruderal forbs, such as *Solanum nigrum,* plus the samples receiving high light and fertility treatments, are positively associated with the light*fertility interaction. The introduced species *Digitalis purpurea* and *Scrophularia nodosa,* and low light–low fertility stands, are negatively associated with the interaction. Extractable potassium was positively correlated with fertilised samples, but only at the lowest light level. Most target species, with the exception of *Silene dioica,* were associated with higher levels of extractable potassium in the soil. *Silene dioica,* plus the spontaneous grasses and other arable weeds, were negatively associated with available potassium. The two high light treatments had significantly lower potassium levels than the most shaded treatment (Section 5.3.2.2). These potassium levels were relatively low, and it is likely that potassium was limiting at higher light levels. The potassium levels in the soil at the end of the experiment reflect the higher biomass and therefore higher nutrient depletion, which has occurred under high light levels.

At higher light levels competitive species are able to adjust their root to shoot ratios in order to optimise nutrient uptake, and when nutrients are available these species are able to swamp other plant strategists and dominate a community. In the present experiment, the spontaneous competitive ruderal forbs and spontaneous grasses, such as *Agrostis stolonifera,* were able to utilise available potassium to their competitive advantage under the 20% and 30% transmitted light treatments. However, these species were light limited under the 5% treatment, and if present at all were unable to make use of soil potassium. In

this low light situation, the competitive advantage lies with the less nutrient-demanding and shade-tolerant woodland species, like *Scrophularia nodosa* (i.e. those species which tend towards stress-tolerant strategies and are able to divert resources to increase light capture). The interaction between light intensity and soil fertility was further investigated, using ANOVA, at community and species levels (Sections 5.3.4-5.3.6).

Mineralisable nitrogen showed no significant correlation with either species or sample distribution in CANOCO (Figure 5.4) or with treatment factors in the ANOVA (Section 5.3.2.2). Levels of mineralisable nitrogen were relatively low and fairly evenly distributed throughout the experiment. As soil nutrients were measured at the end of the experiment and fertiliser additions were made at the beginning, it is probable that much of this highly mobile nutrient had leached from the compost. It is therefore hypothesised that nitrogen limited plant growth throughout the experiment and especially in the two higher light treatments.

The least mobile of the three added macronutrients, phosphorus, although not influencing the vegetation significantly (Figure 5.4), still represents the original fertility treatments, with fertilised samples exhibiting significantly higher concentrations (Section 5.3.2.2). As with potassium a significant light effect also occurred, with greater depletion under higher light environments, i.e. light was inversely proportional to extractable phosphorus (Section 5.3.2.2). However, the apparent lack of effect of extractable phosphorus on the vegetation, perhaps suggests that phosphorus was not yet limiting in this experiment. Therefore, shade appears to influence the degree to which a fertility effect can be realised. This evidence supports the view that fertility has a greater influence on the vegetation before light becomes limiting for non-adapted species, or, conversely, that shade can be used to suppress fertility effects in enriched situations.

A partial RDA model, in which variation due to extractable potassium has been removed, is illustrated in the triplot in Figure 5.6. This model confirms that the light and fertility treatment factors in interaction are positively associated with certain competitive ruderals and negatively associated with stress-tolerant woodland species. Therefore, low light and fertility levels are useful in establishing target ground flora communities. However, the evidence suggests that low light levels negate fertility effects, even in highly fertile environments.

This experiment only tracked the early stages of community development and it is feasible that although light is the key factor in vegetation establishment, fertility may become increasingly important in the longer-term maintenance and evolution of these ground flora communities. When light, and all measurements of it, were partialed out of the RDA model, the fertility treatment variable had the only significant influence on the vegetation, accounting for only 8.4% of the variation in species distribution. Therefore, light regime, and not mineral nutrient supply, is the overriding critical factor influencing plant distribution when species are in competition with each other for resources, in the context of an establishing community.

The RDA biplots of survey 2 and 3 vegetation data shown in Figures 5.7 and 5.8, respectively, chart the progress of community development following the initial weed harvest. As with the 'mature' community, light climate (in the form of PAR) and fertility treatment comprise the two most significant environmental variables, respectively, used to constrain ordinations in both analyses. By comparing the three stages of community development (Figures 5.4, 5.7 and 5.8), it is clear that the arable weed flora declined steadily following its post-harvest resurgence. The initial weed harvest impeded the progress of the arable weed species sufficiently to release the introduced species, which became successively more dominant as the experiment proceeded.

The species distributions in Figures 5.7 and 5.8 appear very similar and represent summer and autumn recording within the same growing season. However, there are some differences between these ordinations and that of the mature community surveyed in the spring of the following season (Figure 5.4). Apart from the decline of the arable weed flora by the final survey, the most significant difference was in the behaviour of the key species *Silene dioica.* This species moved from the darker half of the ordination towards the extreme light end. This move is explained by phenological evidence concerning *Silene* die back under the lowest light treatment, coupled with its apparent competitive edge over the other introduced species in a high light environment. The removal of the initial arable weed community allowed expansion of *Silene* with subsequent niche consolidation and community dominance in the two higher light treatments.

5.3.4 Biomass and height data

The relative contribution of each species to total plant biomass under each of the three light treatments is shown in Table 5.4. The abundance classes used are based on dry biomass data, as opposed to presence / absence vegetation data. As dry biomass data is a more sensitive reflection of environmental effects than non-destructive species abundance data (expressed on the Domin scale), it has been used to produce species abundance tables for the three light treatments, as shown in Table 5.4. *Silene dioica* and *Scrophularia nodosa* dominate communities under the lower two light treatments, whereas in the high light treatment *Agrostis stolonifera* has replaced *Scrophularia nodosa,* which has decreased to an abundance class of 3. It is clear that the most shaded treatment, transmitting only about 5% of PAR, is most favourable for the majority of introduced species. The two exceptions (as identified in the multivariate analyses in Section 5.3.3) are the hedgerow species *Silene dioica* and *Stellaria holostea,* which are favoured by the two higher light environments, transmitting 20% and 30% PAR, respectively.

Plant communities under the lowest light levels are dominated by, and are mostly composed of, introduced woodland species, with a few competitive spontaneous species, occurring at relatively low abundance. The spontaneous woodland species *Rubus fruticosus* agg. is also favoured by the most shaded treatment. In contrast, the two higher light treatments have produced communities, which although dominated by *Silene dioica,* consist of successively greater levels of ruderal forbs and non-woodland grasses, and of successively lower levels of the target ground flora species.

ANOVA results are shown in Table 5.2 for treatment significant biomass and height variables. The leaf area measurements made on the three representative stems of *Silene dioica* and *Scrophularia nodosa* (Section 5.2.3) are also presented in this section. Treatment significant means are either presented in bar charts (Figures 5.9-5.12) or in the table of means (Table 5.3). In all bar charts, means are treatment replicate means. Significant differences between treatment means ($p < 0.05$) are denoted by different letters on top of bars. As species of different origin (Figures 5.9, 5.10, 5.13–5.18) or data from different surveys (Figures 5.22–5.29) were analysed separately, letter coding differs between these groups. Positive standard error bars are shown.

Only dry biomass treatment means are illustrated in Figures 5.9–5.12, as fresh weight results tended to follow similar, but less marked trends (Tables 5.2 and 5.3). Where this is not the case, results are discussed. Figures 5.9 and 5.10 show the mean allocation of the above-ground biomass (dry weight) of the introduced and spontaneously occurring species between the light and fertility treatments (averaged across treatment replicates), respectively. Mean above-ground biomass (of each light treatment replicate) of both introduced and spontaneous species tends to increase with the PAR transmission of the light treatment (Figure 5.9 and Table 5.3). However, only the lowest light treatment shows a significantly lower dry biomass for the introduced species (Figure 5.9) and the fresh weight of the introduced species is greatest under the medium (20% PAR) light treatment (Table 5.3). The results for the total dry weight data (i.e. introduced and spontaneous species combined) follows the same pattern as the dry weight of the introduced species, and the results for total fresh weight mirror those of the fresh weight of the introduced species (Figure 5.9 and Table 5.3). This also supports the use of introduced species biomass data as an indicator of response of the whole vegetation. The reduced biomass of the most shaded treatment illustrates the effect of light limitation on photosynthesis and, therefore, on plant growth. It might be expected that the light-demanding competitive spontaneous species would be most affected by this limitation and also be more able to take advantage of the higher light climate at the other end of the treatment spectrum. This is supported by spontaneous species producing much greater biomass in the high light treatment (30% PAR transmission) (Figure 5.9 and Table 5.3).

Figure 5.10 and Table 5.2 indicates that there was no significant relationship between fertility treatment and biomass, on either the fresh or dry weight of either the introduced or spontaneous species or the total vegetation, although standing biomass visually appears to increase with fertility (Section 5.3.1). This visual difference between fertility treatments was most marked on the early establishment of the ground flora communities after the first weed harvest, and could no longer be distinguished by the end of the experiment. Biomass is, by definition, a response variable measured at the end of the experiment. Fertility effects on density and recruitment (recorded throughout the duration of the experiment) are presented in Section 5.3.5.

The effects of light and fertility treatments on dry biomass of the initial weed harvest are shown in Figures 5.11 and 5.12, respectively. Weed biomass (fresh and dry weight) increased significantly with each successive increase in light level (Figure 5.11 and Table

5.3). This light effect is mirrored in the final harvest biomass of the spontaneous species (Figure 5.9). Removal of the initial weed flora has apparently not effected the response of the spontaneous species to light treatment (Figures 5.9 and 5.11). The lack of fertilisation influence on the dry weed biomass (Figure 5.12) is consistent with that of the final harvest data (Figure 5.10). However, the fresh weed biomass data does show a relationship with fertility treatment (Tables 5.2 and 5.3), being significantly higher in fertilised plots. Removal of the initial weed flora, which was best placed to take advantage of fertility treatments, perhaps diluted any effects on the remaining spontaneous vegetation.

The 'three stem parameters' measured on *Silene dioica* and *Scrophularia nodosa,* including leaf area (Section 5.2.3), make up the remainder of the 'biomass variables'. ANOVA results of treatment significant variables are presented in Table 5.2 and treatment means in Table 5.3. For *Silene dioica,* stem fresh and dry weight and leaf dry weight were all influenced by light treatment (Table 5.2), with biomass increasing with each successively higher light treatment (Table 5.3). Conversely, for *Scrophularia nodosa,* successively higher light treatments produced lower biomass in all variables measured, including leaf area (Table 5.3). This evidence of the opposing niche space, in terms of light climate, occupied by these two species, supports the ecological view of *Silene dioica* as a woodland edge species, able to take advantage of high light situations, and of *Scrophularia nodosa* as a comparatively shade-tolerant woodland herb. The dry stem weight of *Scrophularia nodosa* was also influenced by fertility treatment (Table 5.2), with significantly greater biomass produced at the standard fertilisation rate of N:P:K at 100 kg ha^{-1}, than at 200 kg ha^{-1}, or in unfertilised plots (Table 5.3).

Vegetation stature appeared visually increased under high light–high fertility treatments (Section 5.3.1). This observation was, in part, supported by the statistical evidence presented in Tables 5.2 and 5.3. The mean height of the introduced species was greater in fertilised plots (Table 5.3) and the mean height of the three representative stems of *Silene dioica* was greater under successively higher light regimes. By contrast, *Scrophularia nodosa* mean height decreased with increasing light intensity, mirroring the biomass results for this species (Table 5.3). The above-ground biomass and height evidence suggests that the response of *Silene dioica* was more closely associated with that of the rest of the vegetation, both introduced and spontaneous, than that of *Scrophularia nodosa,* which exhibits an inverse relationship with light intensity. This validates the use of three stems of *Silene dioica* as in some way representative of community response.

5.3.5 Species density and recruitment data

The relative densities of the introduced and spontaneous species under the different light and fertility treatments and at various stages of community development are shown in Figures 5.13-5.20. For practical reasons, reported in Section 5.2.3, only introduced species densities were recorded in survey 4. Figure 5.13 (representing survey 1, i.e. post-weed harvest community establishment) and Table 5.2 show a trend towards higher densities of spontaneous species under the two higher light regimes (20% and 30% PAR irradiance). However, introduced species occurred at significantly greater densities under successively lower light regimes. Introduced stress-tolerant shade species are at a competitive advantage under low light regimes, whereas competitive ruderal spontaneous species tend to dominate in high light environments.

Both introduced and spontaneous species densities were inversely proportional to fertility (Figure 5.14 and Table 5.2). Only the highest level of fertilisation resulted in significantly lower densities of spontaneous species, and densities of introduced species were significantly higher in the control. This inverse relationship could represent an establishment effect, where fertilisation caused osmotic shock to seeds. However, a niche availability effect could be operating, i.e. that plants which establish under high levels of fertility are more likely to grow larger, leaving fewer potential germination niches.

The effects of light and fertility treatments on density data recorded in survey 2 are shown in Table 5.2 and Figures 5.15 and 5.16, respectively. The same trends as observed in survey 1, were exhibited in the survey 2 data (i.e. that the density of introduced species was inversely proportional to light and that density was inversely proportional to fertility), though in survey 2 both fertility treatments resulted in lower densities of spontaneous species. Survey 3 results presented in Table 5.2 and Figures 5.17 and 5.18 follow the same trends as in survey 2. Survey 4 results (which represent introduced species densities at the final harvest) are shown in Table 5.2 and Figures 5.19 and 5.20 and mirror the above trends, with density being inversely proportional to light (all treatments different) and fertility (only two extreme treatments different). A steady decline with time in spontaneous species densities can be observed in Figures 5.13-5.18. A corresponding, but less marked, increase occurs in numbers of introduced species (Figures 5.13-5.20). This indicates that overall experimental conditions favoured introduced rather than spontaneous species.

A significant interaction between the treatment factors was detected in introduced species density data from surveys 1–3 (Figure 5.21), which became statistically weaker with time (Table 5.2). In unfertilised samples with a high light environment densities of introduced species were significantly reduced. In the two fertilised treatments densities were generally different under the high and low light treatments. Low levels of light and fertility generally favour introduced species. Figure 5.21 illustrates that the lowest light treatment (5% PAR) always favours introduced species. At 5% and 20% PAR transmission fertilisation will reduce the success of the introductions, presumably due to increased competition from spontaneous species (Figures 5.13-5.18), whereas, at 30% PAR fertilisation at the standard 100 kg ha^{-1} application rate appears to enhance success of the introduced species. The progressive weakening of the treatment interaction emphasises the importance of establishment environment, as predicted by Cohn (1994).

Table 5.2 and Figures 5.22 and 5.23 show, respectively, the influence of light and fertility on the recruitment of introduced species between surveys. During the initial establishment of the ground flora communities (survey 1-2) light had a significant effect on recruitment, with greater seedling recruitment occurring under the two lowest light regimes (5% and 20% PAR). Recruitment of introduced species was inversely proportional to fertility, with significantly higher recruitment in unfertilised plots. Little recruitment occurred between surveys 2 and 3, and no treatment effects were observed. Seedling recruitment between surveys 3 and 4 (representing late development of ground flora communities), although substantial in numbers, was not significantly affected by either light or fertility treatment. Low levels of light and fertility favour recruitment of the introduced target species. The influences of both light and fertility on recruitment, were only significant between surveys 1 and 2, further supporting the view of Cohn (1994) that environmental conditions at establishment are crucial to the success of introduced species.

5.3.6 Individual species density data

Information about the behaviour of individual species which dominate or form an important part of the experimental ground flora communities is gained from density data recorded throughout the experiment, and is shown in Figures 5.24-5.29 and Tables 5.2 and 5.3. Only those species that consistently exhibited significant treatment effects on their density, throughout the experiment, are shown in Figures 5.24-5.29; other notable results are discussed at the end of this section.

Table 5.2 and Figures 5.24 and 5.25 show the effect of light and fertility treatments, respectively, on *Silene dioica* densities recorded in the four surveys. Light had no significant effect on *Silene* density. Density was inversely proportional to fertility, with significantly greater numbers of *Silene* plants in unfertilised boxes. This inverse relationship between density and fertility was also found with *Scrophularia nodosa* densities (Figure 5.27). Fertility ceased to significantly influence the later stages of community consolidation by this species, i.e. in survey 4 (Table 5.2). The density distribution of *Scrophularia* was influenced by light even more than fertility (Table 5.2). Figure 5.26 shows that density was negatively correlated with light. *Scrophularia* density was always different under the highest and lowest light treatments and was different under all three light treatments in surveys 3 and 4.

The density of *Brachypodium sylvaticum* was affected throughout the experiment by light, but only by fertility at establishment (Tables 5.2 and 5.3 and Figure 5.28). *Brachypodium* density was influenced by light in a similar way to *Scrophularia* (i.e. plant density was higher at lower light levels and significantly greater in the lowest light treatment (5% PAR), except in survey 4). *Brachypodium* density was inversely influenced by fertility at establishment, with higher densities occurring in unfertilised plots (Tables 5.2 and 5.3).

Digitalis purpurea, although not significantly influenced by light climate (Table 5.2), was affected by fertility treatment (Table 5.2 and Figure 5.29). The highest level of fertilisation significantly restricted plant numbers. Table 5.2 indicates that this fertility effect seems more important at the end of the experiment than at establishment, contrary to most of the species density results. Few other treatment effects were observed on the densities of individual species.

A light effect was identified on *Stellaria holostea* and *Circaea lutetiana* in survey 4 (Tables 5.2 and 5.3). *Circaea lutetiana* grew at higher densities under the lowest light treatment and *Stellaria holostea* densities increased under successively higher light regimes (Table 5.3). *Stellaria holostea* was the only introduced species to have a positive relationship with light intensity, however Table 5.2 shows that plot position effect was as important. *Viola riviniana* densities were reduced by fertilisation in survey 3 (Tables 5.2 and 5.3). Densities of *Primula vulgaris* were inversely proportional to fertility treatment (Tables 5.2 and 5.3). *Bromopsis ramosa* grew at greater densities under the lowest light treatment (5% PAR) in survey 2 (Tables 5.2 and 5.3). No significant treatment interactions, where both main

effects were significant, were detected in the individual species density data (Table 5.2). Although these data provide useful information about how key species utilise resources (e.g. the fact that the dominant *Silene dioica* is only affected by fertility (Table 5.2) as opposed to the generally more influential light factor) ANOVA results from the entire vegetation, as discussed in Section 5.3.3, are perhaps more useful in interpreting community composition and function.

5.4 Discussion

Light climate has a highly significant influence on the direction of vegetation development, and can therefore be regarded as being a major determinant of field layer development in artificial ground flora communities, within a controlled environment. If these artificial communities are regarded as functional representations of woodland ground flora communities, then the evidence from this experiment supports Packham *et al.* (1992), in regarding light as usually being the most limiting factor for field layer herbs.

Throughout the experiment, the evidence gained through the statistical modelling of the multivariate vegetation data (Figures 5.3-5.4 and 5.7-5.8) showed that light, measured as a percentage of ambient PAR, represented the most important axis of variation in the data. Light treatment produced the only significant influence on the more sensitive biomass data, with positive correlations between light intensity and biomass of both introduced and spontaneous species (Figure 5.9). The physiognomy (Plate 5.3) also supports this view, with light treatment being the most apparent determinant of community type (Table 5.4). However, this experiment was designed to investigate the influence of both light intensity and soil fertility on ground flora development, and to focus on the interaction between the two factors.

Evidence from CANOCO analyses for the second axis of variation in the data representing a fertility gradient was less convincing than that for the light axis. However, the fertility treatment did produce a secondary influence on the plant communities (Figures 5.2-5.4 and 5.7-5.8). The measured components of fertility had no statistically significant influence on the vegetation, though extractable potassium had an underlying influence when the two treatment factors were considered in combination as an interaction (Figures 5.5 and 5.6). ANOVA results support the potassium influence, with potassium concentrations at the end of the experiment closely linked with light intensity (Table 5.3). Potassium depletion by the ground flora plants occurred where light was not limiting. However, as light became

limiting, at about 5% PAR, adapted plants diverted resources towards light capture and non-shade plants failed to utilise resources and lost their competitive advantage. Although no statistical interaction between light and fertility treatments was detected on potassium concentrations, the treatments are seen to act in combination, with maximum nutrient uptake occurring under the standard fertilisation rate of 100 kg ha^{-1}.

No effects on vegetation of the other two macronutrients were observed. Any effect of nitrogen addition would have been temporary due to the relative mobility of this nutrient. However, a short-lived nitrogen effect, using mineralisable nitrogen as an indicator, would not have been detectable in the ANOVA as soil properties were only measured at the end of the experiment. Any short-lived nitrogen effect would have had greatest influence on the initial arable weed communities, which were harvested to allow desirable progression of the experiment. Nevertheless, no fertility treatment effect was detected on the initial weed biomass (Figure 5.12). Concentrations of extractable phosphorus (the least mobile of the measured macronutrients) mirrored fertility treatments at the end of the experiment, and uptake was clearly limited, as was that of potassium, at 5% PAR infiltration (Table 5.3). However, no significant effects of extractable phosphorus on the vegetation were detected in the multivariate analyses (Section 5.3.3). It seems likely that nitrogen was limiting throughout the experiment and that phosphorus was never limiting. Although potassium itself may not have been limiting during this experiment, the limiting effect of light impeded its uptake by plants (i.e. light was acting in combination with at least one aspect of soil fertility in the form of extractable potassium).

The species density data provides statistical evidence of the influence of light intensity and soil fertility in combination and in interaction, at the community level. The significant effects of both treatments on the introduced and spontaneous species density data (Section 5.3.5) demonstrates how light intensity and soil fertility act in combination, and may suggest an interaction between the two factors. Introduced species density was inversely proportional to light and fertility (Figures 5.13–5.20) and spontaneous species density differed in being proportional to light (Figures 5.13-5.18). During the first growing season (1999) (i.e. surveys 1-3) a significant interaction between the treatments, representing light intensity and soil fertility, was detected on the introduced species density data (Figure 5.21). At high light levels (30 % of ambient PAR) with no fertiliser additions, fertility depletion and niche consolidation effects were observed with significantly lower densities of introduced species compared to other treatment combinations. These effects on the

introduced species were compounded by maximum competition from spontaneous species (Figures 5.13, 5.15, 5.17). In the two fertilised treatments, introduced species were more successful under the lowest light treatment. Although fertilisation appears to adversely affect the density of the introduced species at 5% and 20% PAR by favouring spontaneous competition, at 30 % PAR, fertilisation of 100 kg ha^{-1} appears to enhance the success of the introduced species. This effect appears most important at establishment, where fertilisation appears in part to negate the adverse impact on the introduced species of a high light environment. This could be because fertility depletion under high light environments is likely to negatively affect introduced as well as spontaneous species. However, no such interaction between treatment factors was detected in the density response of the spontaneous species (Table 5.2).

When light is not limiting (i.e. above 5% PAR) fertility depletion, probably in the form of potassium, occurs (Plate 5.3), but as light becomes limiting plants are unable to utilise the soil mineral resource and fertility becomes less relevant. Excess fertility is a potential problem for woodland ground flora herbs experiencing light levels of around 20% and 30% of ambient PAR, due to enhanced competition from non-shade-tolerant species. At the highest light levels, a moderate dose of fertiliser may improve the establishment chances and subsequent competitive success of the woodland herbs. Cohn (1994) found that, once established, woodland introductions compete well with spontaneous ground flora, even under high light conditions. *Silene dioica,* which dominates these higher light communities, may well provide a surrogate canopy for the more stress-tolerant woodland herbs in the longer-term.

The recruitment evidence (Section 5.3.5) showed that light intensity and fertility inversely affected the recruitment of seedlings of introduced species during the early establishment of the post-weed harvest ground flora communities (Figures 5.22 and 5.23). Seedling recruitment of introduced species was optimised under low and medium light regimes (5% and 20% PAR infiltration) and no fertilisation. No treatment interaction was evident in the recruitment data (Table 5.2). The recruitment evidence emphasises the importance of the establishment environment.

The autecological evidence gained from the individual species density data and the 'three stem parameters', may provide further clues as to how and when light intensity and soil fertility interact. The density of the community dominant *Silene dioica* was not affected by

light treatment (Figure 5.24). However, the biomass of this species was proportional to light intensity (Tables 5.2 and 5.3). Conversely, *Silene* density was inversely proportional to fertility throughout the experiment (Figure 5.25), whereas *Silene* biomass was unaffected by fertility treatment (Table 5.2). This evidence perhaps suggests differing strategies of this species at different ends of different resource spectrums. Where resources are not limiting, *Silene* can take advantage by enhanced growth. This species does not appear to be limited in establishment terms by light climate (Figure 5.24), but niche consolidation will be limited at the lowest light levels. Niche consolidation and accompanying nutrient depletion in fertilised plots is mirrored by enhanced establishment in control plots (Figure 5.25). This supports the work of Cohn (1994), who found that *Silene* responded positively to nutrient addition when light was limiting and to increased irradiance when mineral nutrient supply was limiting. As *Silene dioica* initially dominated all communities (and although the species experienced a later marked decline under the lowest light treatment, it was still co-dominant here with *Scrophularia nodosa* (Table 5.4)), it is probable that the observed fertility depletion and niche colonisation effects would have been most marked for this species.

The co-dominant species *Scrophularia nodosa* exhibits the same relationship between density and soil fertility (Figure 5.27), but is perhaps more strongly influenced by light intensity (Figure 5.26), which is inversely proportional to density. This inverse relationship with light intensity was also evident in the biomass data for this species (Section 5.3.4). The fact that *Scrophularia nodosa* was more influenced by light intensity compared to *Silene dioica* illustrates that *Scrophularia* is a more shade-tolerant plant and that *Silene* is tolerant of a far wider range of light conditions, supporting the work of Slade and Causton (1979), Sinker *et al.* (1991) and Grime *et al.* (1988). The ability of *Silene dioica* to tolerate the range of light climates simulated in this experiment explains why this species is more influenced by fertility levels. Farley and Fitter (1999b) found that *Silene dioica*, not only responded positively to nutrient-rich soil patches, but was sensitive to the nutrient concentration of the patch.

The influence of light on *Brachypodium sylvaticum* throughout the experiment (Figure 5.28) demonstrates the shade-tolerance of this woodland grass. Whereas *Digitalis purpurea,* which was only affected by fertility treatment (Figure 5.29), is not highly shade-tolerant and tends to be associated with rides and clearings in woodland (Sinker *et al.*, 1991). The hedgerow species *Stellaria holostea* was unique, in this experiment, in being

positively associated with light intensity with respect to density. Although certain species are clearly influenced by both light intensity and soil fertility, no interactions between the two factors (where both main effects were significant) were detected in the autecological data.

In summary, light intensity was the major determinant of field layer development in artificial ground flora communities. The effects of fertility were very much secondary and governed by light climate at the community level. In general terms, biomass parameters were most influenced by light treatment, whereas density parameters (including recruitment) were affected by both light and fertility treatment (Table 5.2). Interaction between light intensity and soil fertility was detectable at the community level in the density of the introduced species. Certain results from the individual species density and biomass data were not dissimilar to autecological studies (e.g. Cohn, 1994; Farley and Fitter, 1999b), suggesting that perhaps experimental design had minimised inter-specific competition effects, permitting a largely 'autecological response' from the introduced species.

The results indicate that the design of this experiment was suitable for, and the best way of achieving the experimental aims. The lack of block significance on the environmental and response variables (Table 5.2) demonstrates that background environmental conditions within the polytunnel were sufficiently uniform to allow their elimination by the experimental design, in stark contrast to field Experiment 2. The spacing of samples and species in ordination space in the RDA (Figure 5.4) shows that the light and fertility treatments were conducive to producing a measurable and meaningful range of environmental responses from both introduced and spontaneous species. The physiognomy (Plate 5.2) and vegetation data, over time (Figures 5.7, 5.8, 5.4), illustrates that the initial weed harvest was sufficient to 'knock back' the undesirable arable weeds and allow the establishment and niche consolidation of the introduced woodland species. The post-weed harvest species density data (Figures 5.13-5.18) shows that the experimental conditions favoured the introduced species over the spontaneous species. When extrapolating results from artificial ground flora communities to those in the field, it seems unlikely that weeds would pose so serious a problem in the less competitive environment of a secondary woodland, as even after thinning or in new plantations, shade (whether it be from the tree canopy or a 'nurse' tall herb canopy) will eventually cause competitive exclusion of these species.

5.5 Conclusions

- Light intensity was the major determinant of field layer development in the artificial ground flora communities created in the polytunnel.

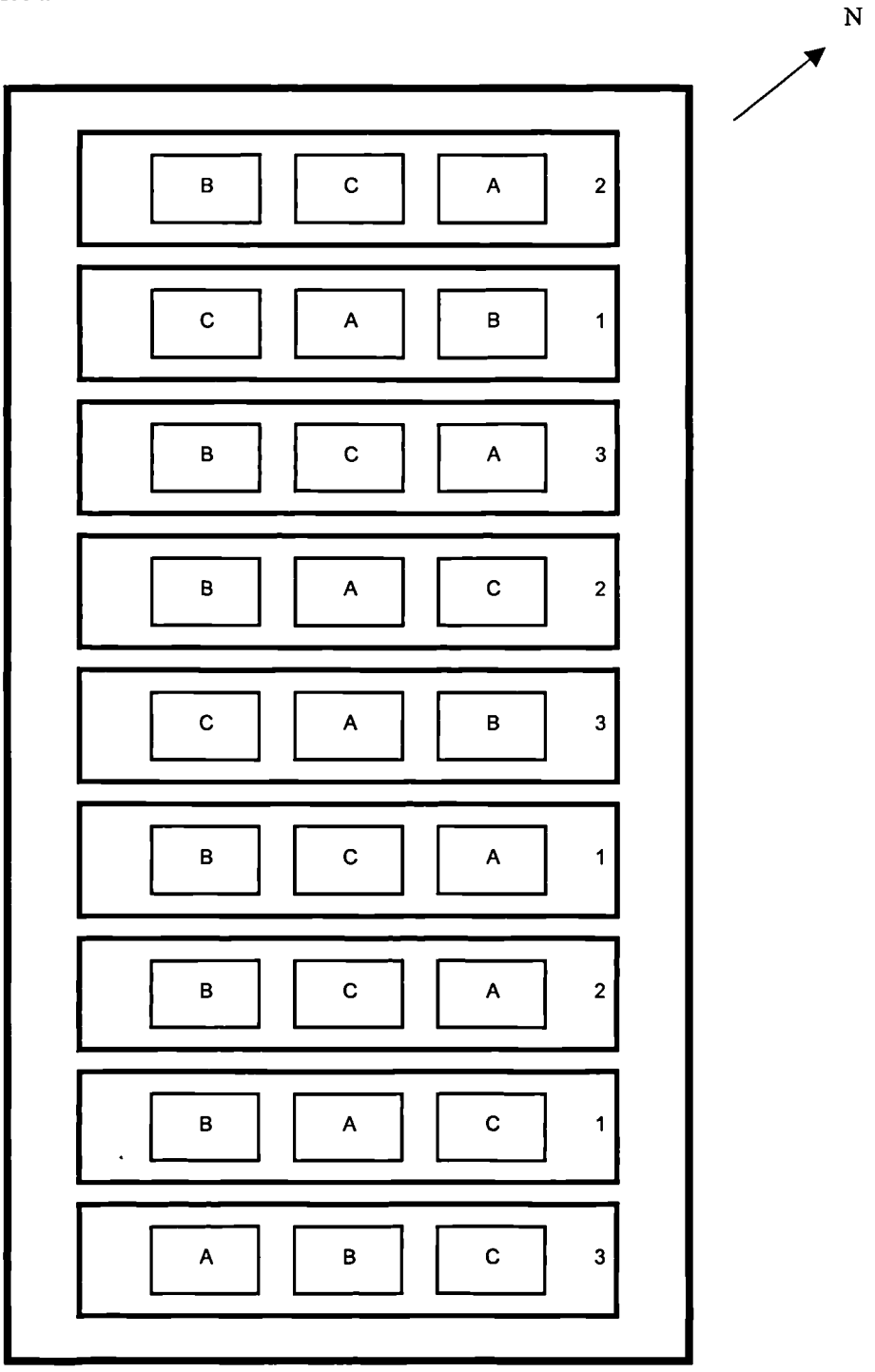
- Soil fertility was a significant determinant of field layer development in the artificial ground flora communities of Experiment 3; however, its influence was very much secondary to that of the light climate, and ceased to be significant when measured in its component parts.

- The influence of soil fertility and light intensity was complex, as different factors exerted influence on different components of the community at different stages of development. For example, low fertility and light levels were important for seedling recruitment of target species during establishment and early community development and light appeared to be the controlling factor on the biomass parameters which represented full community development.

- Light intensity and soil fertility acted both singly and in combination at the community level. There was also statistical evidence to support a direct interaction between soil fertility and light climate. There was some evidence to suggest that soil fertility had greatest influence before light become limiting, after which shade negated its effects.

- In general terms, Experiment 3 suggests that woodland introductions are likely to be favoured by low levels of light and fertility (i.e. about 5% of ambient PAR levels and unfertilised low fertility compost) when in competition with arable weeds and vigorous grasses, in artificial plant communities. However, fertilisation with 100 kg ha^{-1} N:P:K compound agricultural fertiliser did not appear to detrimentally affect the establishment of introduced woodland species and helped them compete with spontaneous species under high light regimes (about 30% PAR infiltration).

Figure 5.1 Layout of Experiment 3: the soil fertility and light manipulation experiment in the polytunnel at the Plant Environment Research Unit.



Key:	Light level		Fertility level	
	1	Low	A	Low = Control
	2	Medium	B	Medium = 100 kg ha^{-1} N:P:K compound fertiliser
	3	High	C	High = 200 kg ha^{-1} N:P:K compound fertiliser

Plate 5.1 Photographs of Experiment 3, taken on 04/03/99 showing: (a) Establishment. The form and layout of the light treatments can clearly be seen. (b) Initial germination. The three seedbank trials can be seen in the foreground. In the background light tents are open to reveal the arrangement of soil boxes within.

(a)

(b)

Plate 5.2 Sequential photographs of a typical sample box from Experiment 3 (medium light, 20% PAR - medium fertility, 100kg ha^{-1} N:P:K), illustrating the development of the experimental ground flora communities, from (a) initial germination (04/03/99) and (b) early development of the arable weed flora dominated by *Fumaria officinalis* (10/05/99), through to (c) establishment of the post-weed harvest ground flora communities (12/08/99) and (d) their maximum development (30/04/00).

(a)

(b)

(c)

(d)

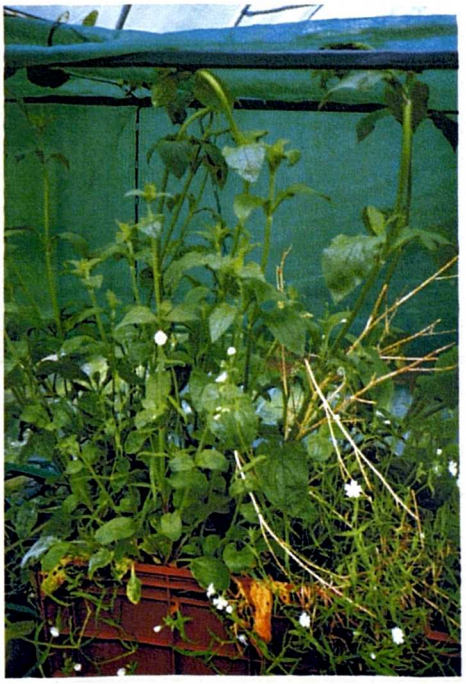
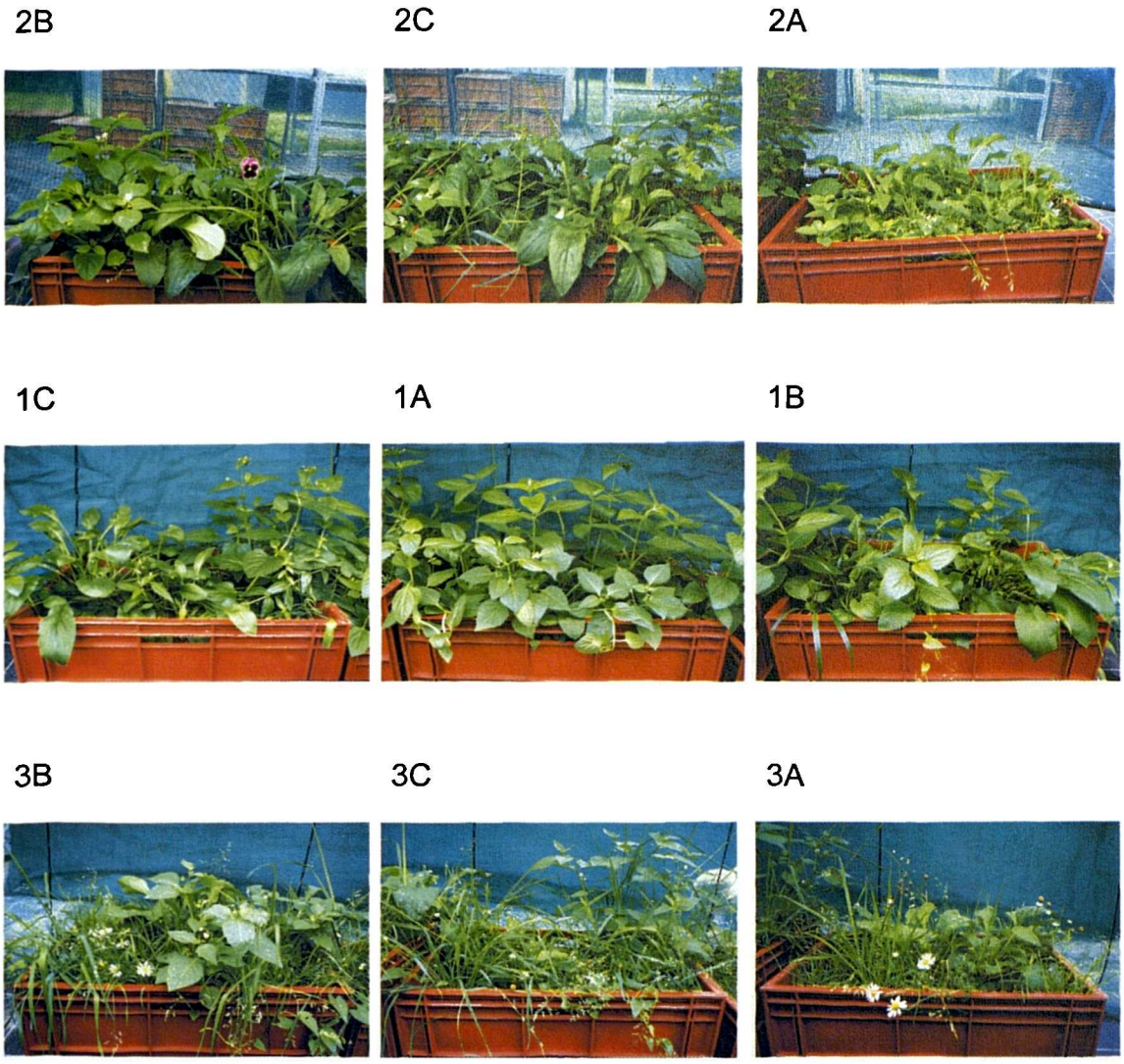


Plate 5.3 Photomontage of the first replicate of Experiment 3: the soil fertility and light manipulation experiment in the polytunnel at the Plant and Environment Research Unit, taken on 12/08/99, showing the establishment and early development of the post-weed harvest ground flora communities.



Key:	Light Level		Fertility Level	
	1	Low	A	Low = Control
	2	Medium	B	Medium = 100 kg ha^{-1} N:P:K fertiliser
	3	High	C	High = 200 kg ha^{-1} N:P:K fertiliser

Table 5.2: ANOVA Table showing treatment significant variables in Experiment 3.

		Mean Squares of variables with significance levels							
Source of variation	d.f.	Axis1 t		PAR		Ext K t		Ext P	
Block	2	0.484	ns	9.521	ns	0.006179	ns	60.09	ns
Light	2	6.355	**	1120.7	***	0.5983	***	412.7	***
Fertility	2	0.1072	ns	0.755	ns	0.04595	*	797.6	***
Light*Fertility	4	0.6571	ns	1.263	ns	0.01881	ns	30.57	ns
Residual	16	0.655		2.795		0.009117		38.09	

		Means Squares of variables with significance levels					
Source of variation	d.f.	pH		OM		Height Intro	
Block	2	0.02866	ns	1.806	ns	3.2	ns
Light	2	0.04841	ns	10.75	*	104.4	ns
Fertility	2	0.2158	**	0.147	ns	704.1	*
Light*Fertility	4	0.04051	ns	2.318	ns	281.8	ns
Residual	16	0.02524		2.115		134.5	

		Means Squares of variables with significance levels							
Source of variation	d.f.	FW Intro		DW Intro		FW Spon t		DW Spon t	
Block	2	137311	ns	2400	ns	7.687	ns	2.64	ns
Light	2	1173518	**	35238	***	34.12	**	25.36	***
Fertility	2	95389	ns	1087	ns	3.289	ns	0.595	ns
Light*Fertility	4	142181	ns	1296	ns	3.962	ns	1.5	ns
Residual	16	132319		3237		5.49		1.047	

		Means Squares of variables with significance levels							
Source of variation	d.f.	FW Total		DW Total		FW Weed		DW Weed	
Block	2	161903	ns	3967	ns	420.2	ns	1.229	ns
Light	2	1192997	**	45198	***	72873.4	***	1151.4	***
Fertility	2	84016	ns	726	ns	1352.2	**	5.253	ns
Light*Fertility	4	140990	ns	1114	ns	367.2	ns	1.585	ns
Residual	16	124214		2664		209.7		3.65	

		Means Squares of variables with significance levels							
Source of variation	d.f.	Silene Height		Sile leafDWt		Sile stemFWt		Sile stemDWt	
Block	2	169.7	ns	0.1188	ns	2.678	ns	0.1061	ns
Light	2	4492.5	**	0.5445	*	18.63	***	3.871	***
Fertility	2	523.2	ns	0.1365	ns	1.36	ns	0.2614	ns
Light*Fertility	4	638.3	ns	0.1033	ns	1.683	ns	0.2723	ns
Residual	16	520.9		0.136		1.704		0.2668	

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively. ns: not significant. t: transformed data.

FW: fresh weight (g). DW: dry weight (g). LA: leaf area (cm^2).

Intro: introduced species. Spon: spontaneous species. OM: soil organic matter (%).

Table 5.2: ANOVA Table showing treatment significant variables in Experiment 3.

		Means Squares of variables with significance levels			
Source of variation	d.f.	Scroph Height	Scroph LAt	Scro leafFWt	Scro leafDWt
Block	2	9.9 ns	2.3 ns	0.006 ns	0.00297 ns
Light	2	4609.7 ***	582.0 ***	7.045 ***	0.7054 **
Fertility	2	541.1 ns	75.38 ns	1.90 ns	0.1866 ns
Light*Fertility	4	471.2 ns	48.62 ns	0.8952 ns	0.1189 ns
Residual	16	292.4	31.18	0.6038	0.08908

		Means Squares of variables with significance levels	
Source of variation	d.f.	Scro stemFWt	Scro stemDWt
Block	2	0.0432 ns	0.0064 ns
Light	2	6.775 **	0.6213 *
Fertility	2	1.893 ns	0.4436 *
Light*Fertility	4	1.148 ns	0.303 ns
Residual	16	0.6894	0.1079

		Means Squares of variables with significance levels			
Source of variation	d.f.	Den Intro 1	Den Intro 2	Den Intro 3	Den Intro 4
Block	2	26.7 ns	18.04 ns	6.33 ns	25.5 ns
Light	2	340.6 ***	628.7 ***	654.3 ***	1309.1 ***
Fertility	2	213.6 ***	591.3 ***	505.3 ***	689.6 *
Light*Fertility	4	75.04 **	112.3 *	94.17 *	94.7 ns
Residual	16	15.66	31.0	24.25	114.6

		Means Squares of variables with significance levels			
Source of variation	d.f.	Den Spon 1	Den Spon 2t	Den Spon 3	Rec Intro 1-2t
Block	2	3344 ns	0.05874 ns	292.3 ns	0.546 ns
Light	2	5983 *	0.4436 ***	5489.0 ***	4.413 *
Fertility	2	4317 *	0.192 **	1117.1 ***	4.419 *
Light*Fertility	4	674 ns	0.02814 ns	286.4 ns	0.682 ns
Residual	16	1122	0.01986	103.8	1.214

		Means Squares of variables with significance levels			
Source of variation	d.f.	Brac sylv 1	Brac sylv 2	Brac sylv 3	Brac sylv 4
Block	2	5.48 ns	1.37 ns	0.481 ns	0.481 ns
Light	2	103.7 **	28.7 ***	27.37 ***	18.82 **
Fertility	2	97.81 **	1.593 ns	1.815 ns	7.815 ns
Light*Fertility	4	30.48 ns	3.259 ns	2.037 ns	2.593 ns
Residual	16	13.9	1.412	1.606	2.19

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively. ns: not significant. t: transformed data.

FW: fresh weight (g). DW: dry weight (g). LA: leaf area (cm^2). Den: density.

Intro: introduced species. Spon: spontaneous species. Rec: recruitment.

All density data for individual species denoted by abbreviated Latin names.
Numbers following variable names denote survey number.

Table 5.2: ANOVA Table showing treatment significant variables in Experiment 3.

		Means Squares of variables with significance levels			
Source of variation	d.f.	Brom ramo 2t	Circ lute 4	Digi purp 2t	Digi purp 3t
Block	2	0.327 ns	5.78 ns	0.2031 ns	0.5887 ns
Light	2	1.013 *	148.8 *	1.281 ns	1.418 ns
Fertility	2	0.327 ns	25.44 ns	4.455 **	3.29 **
Light*Fertility	4	0.5262 ns	48.56 ns	1.543 *	1.288 ns
Residual	16	0.2335	37.78	0.4577	0.5211

		Means Squares of variables with significance levels			
Source of variation	d.f.	Digi purp 4t	Prim vulg 2t	Prim vulg 3t	Prim vulg 4t
Block	2	0.4636 ns	0.1021 ns	0.0931 ns	0.037 ns
Light	2	0.8013 ns	0.4164 ns	0.5185 ns	0.1021 ns
Fertility	2	3.482 ***	0.8608 *	1.101 *	0.9529 *
Light*Fertility	4	0.6413 ns	0.3608 ns	0.3749 ns	0.4719 ns
Residual	16	0.3392	0.2271	0.2699	0.2353

		Means Squares of variables with significance levels			
Source of variation	d.f.	Scro nodo 1	Scro nodo 2	Scro nodo 3	Scro nodo 4
Block	2	5.48 ns	7.26 ns	7.26 ns	10.78 ns
Light	2	103.7 **	103.6 ***	110.5 ***	406.8 ***
Fertility	2	97.81 **	104.9 ***	111.8 ***	119.4 ns
Light*Fertility	4	30.48 ns	22.98 ns	21.48 ns	47.72 ns
Residual	16	13.9	10.13	10.22	34.24

		Means Squares of variables with significance levels			
Source of variation	d.f.	Sile dioi 1	Sile dioi 2t	Sile dioi 3	Sile dioi 4t
Block	2	12.48 *	0.2947 ns	10.04 **	0.01644 ns
Light	2	8.926 ns	0.1857 ns	4.926 ns	0.02212 ns
Fertility	2	15.15 *	0.979 ***	17.15 ***	0.1124 **
Light*Fertility	4	6.926 ns	0.56 **	9.704 **	0.1256 ***
Residual	16	2.481	0.08954	1.37	0.01712

		Means Squares of variables with significance levels	
Source of variation	d.f.	Stel holo 4	Viol rivi 3t
Block	2	4.037 *	0.0817 ns
Light	2	3.593 *	0.6889 ns
Fertility	2	0.9259 ns	2.027 *
Light*Fertility	4	0.2037 ns	0.2487 ns
Residual	16	0.7454	0.5418

*, **, ***: $p < 0.05, 0.01, 0.001$, respectively. ns: not significant. t: transformed data.

All density data for individual species denoted by abbreviated Latin names.

Numbers following variable names denote survey number.

Table 5.3: Table of Means of treatment significant variables in Experiment 3.

	Means of variables per light treatment replicate				
Light treatment	Axis1 t	PAR	Ext Kt	Ext P	OM
5	-0.96	6.5	194.1	41.8	13.7
20	0.35	18.5	68.7	30.6	11.6
30	0.6	28.8	70.1	29.6	12.1
Standard Error	0.27	0.56	0.032	2.1	0.49

	Means of variables per light treatment replicate				
Light treatment	FW Intro	FW Spon t	FW Total	DW Total	FW Weed
5	296.0	15.76	321.0	43.9	14.0
20	1001.0	19.45	1021.0	163.1	163.1
30	786.0	56.85	847.0	169.9	175.8
Standard Error	121.3	0.78	117.5	17.2	4.8

	Means of variables per light treatment replicate				
Light treatment	Silene Height	SileleafDWt	SilestemFWt	SilestemDWt	Scroph Height
5	48.7	0.72	3.13	0.3	69.8
20	82.6	1.28	14.06	2.25	45.3
30	90.9	1.78	20.79	3.28	24.6
Standard Error	7.6	0.12	0.44	0.17	5.7

	Means of variables per light treatment replicate				
Light treatment	Scroph LAt	ScroleafFWt	ScroleafDWt	ScrostemFWt	ScrostemDWt
5	561.7	8.58	0.97	7.29	0.78
20	207.4	3.61	0.63	3.96	0.66
30	59.3	1.37	0.19	0.94	0.16
Standard Error	1.9	0.26	0.1	0.28	0.11

	Means of variables per light treatment replicate		
Light treatment	Brom ramo 2t	Circ lute 4	Stel holo 4
5	0.6	7.4	0.6
20	0.1	0.9	0.9
30	0.0	0.0	1.8
Standard Error	0.16	2.1	0.29

t: ANOVA performed on transformed data. FW: fresh weight (g). DW: dry weight (g).

LA: leaf area (cm^2). Intro: introduced species. Spon: spontaneous species.

All density data for individual species denoted by abbreviated Latin names.

OM: soil organic matter (%). Numbers following variable names denote survey number.

Table 5.3: Table of Means of treatment significant variables in Experiment 3.

	Means of variables per fertility treatment replicate		
Fertility treatment	Ext Kt	Ext P	pH
0	81.3	23.6	5.4
100	103.8	36.5	5.2
200	110.9	41.9	5.1
Standard Error	0.032	2.1	0.053

	Means of variables per fertility treatment replicate		
Fertility treatment	Height Intro	FW Weed	ScrostemDWt
0	32.1	103.5	0.3
100	47.7	124.1	0.91
200	47.1	125.4	0.36
Standard Error	3.9	4.8	0.11

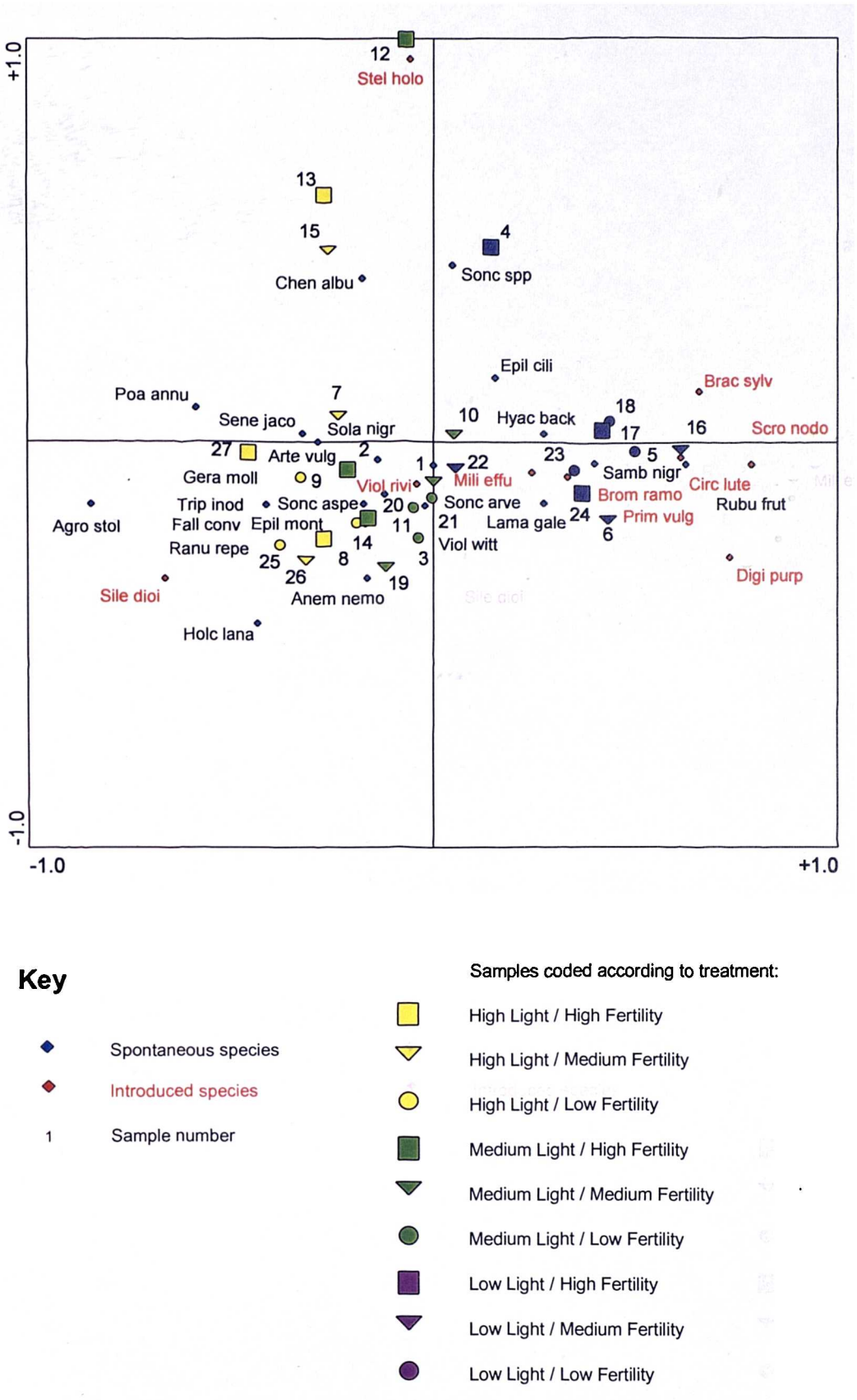
	Means of variables per fertility treatment replicate				
Fertility treatment	Brac sylv 1	Prim vulg 2t	Prim vulg 3t	Prim vulg 4t	Viol rivi 3t
0	10.1	0.4	0.5	0.4	1.9
100	6.2	0.2	0.2	0.1	0.3
200	3.6	0.0	0.0	0.0	0.3
Standard Error	1.2	0.16	0.17	0.16	0.25

t: ANOVA performed on transformed data. FW: fresh weight (g). DW: dry weight (g).

LA: leaf area (cm^2). Intro: introduced species. Spon: spontaneous species.

All density data for individual species denoted by abbreviated Latin names.

Numbers following variable names denote survey number.



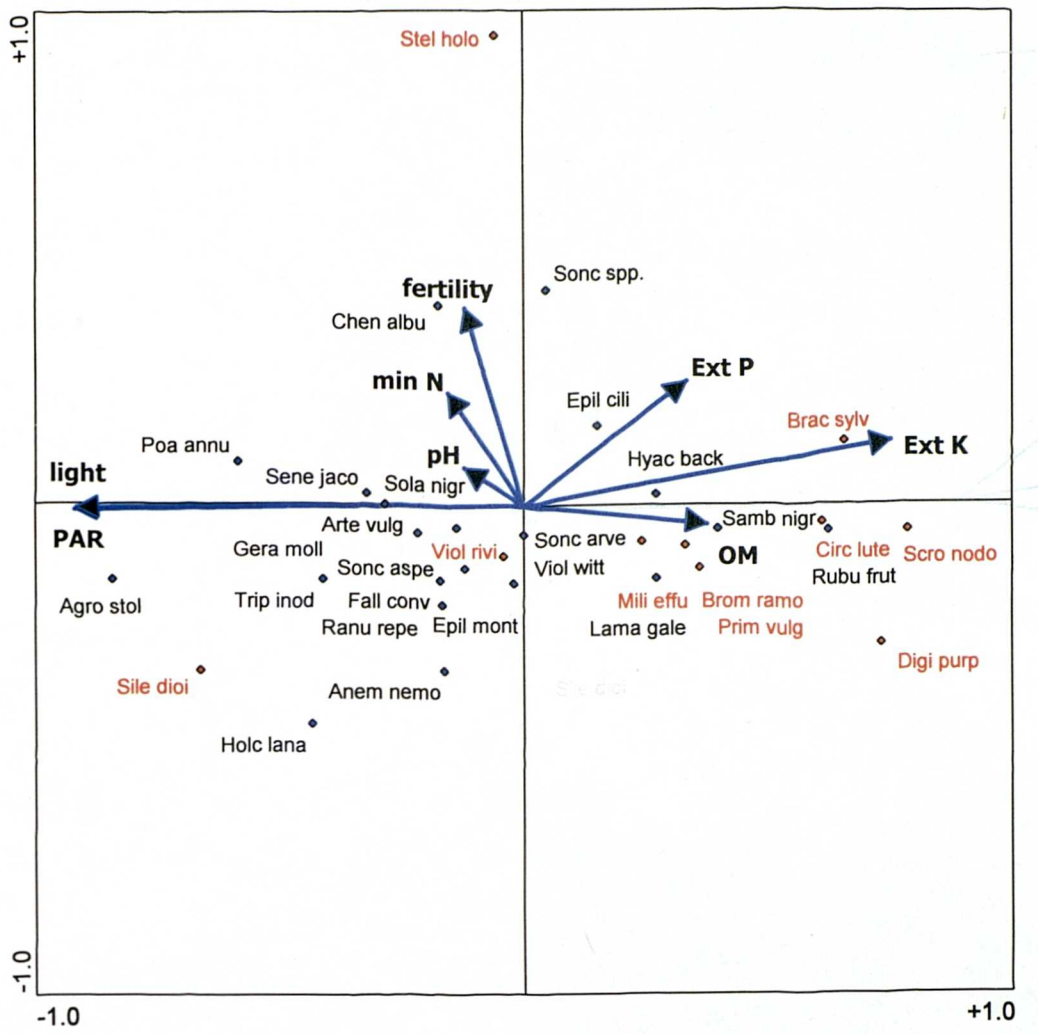
Key

- Spontaneous species
- Introduced species
- 1 Sample number

Samples coded according to treatment:

- High Light / High Fertility
- High Light / Medium Fertility
- High Light / Low Fertility
- Medium Light / High Fertility
- Medium Light / Medium Fertility
- Medium Light / Low Fertility
- Low Light / High Fertility
- Low Light / Medium Fertility
- Low Light / Low Fertility

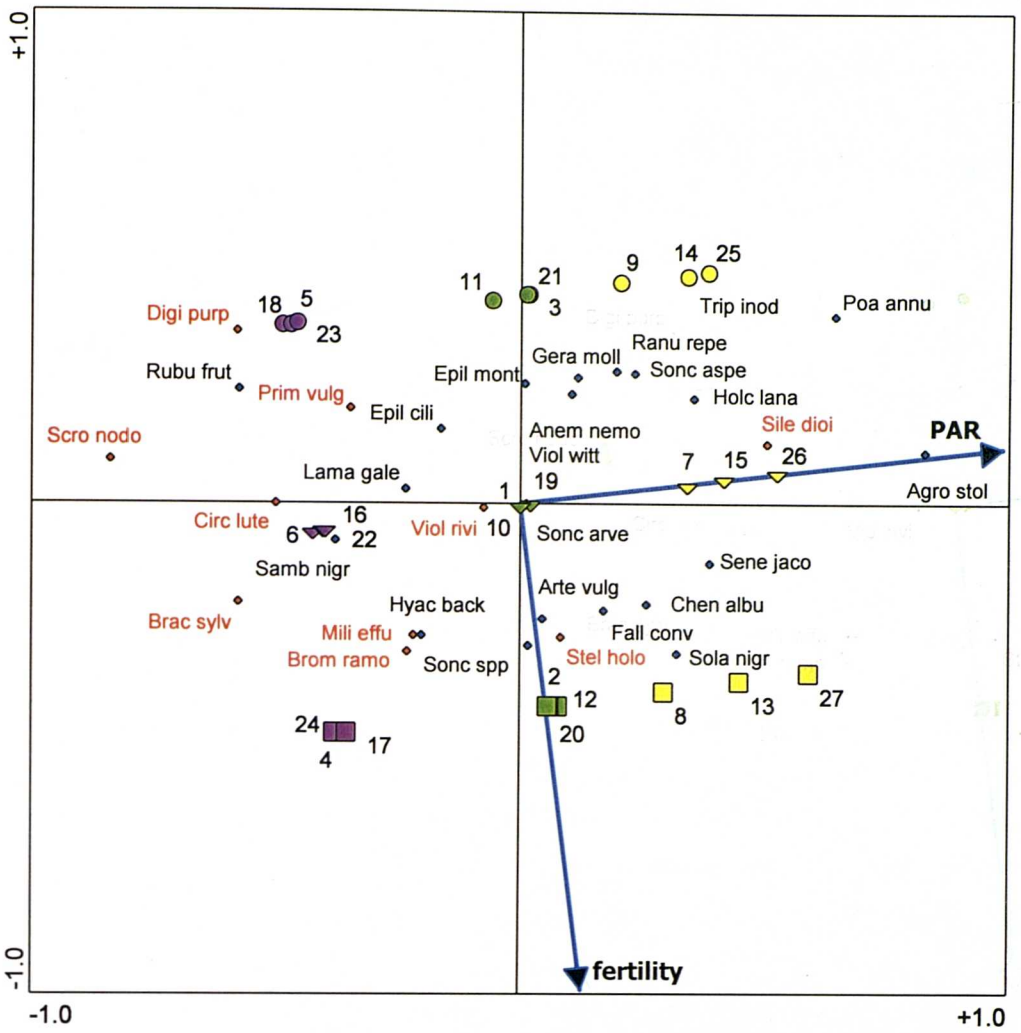
Figure 5.2 Species and sample scatter plot of the first two axes from PCA on the pre-harvest vegetation data of Experiment 3. This shows the distribution of the vegetation relative to treatment and sample position. Light treatments are colour coded and fertility treatments are coded by shape. Introduced and spontaneous species are distinguished.



Key

- Spontaneous species
- Introduced species
- Environmental variable
- **OM** Soil organic matter

Figure 5.3 Species scatter plot of the first two axes from PCA on the pre-harvest vegetation data of Experiment 3, on to which passive environmental variables have been superimposed. This shows the distribution of the vegetation relative to the environmental variables. Introduced and spontaneous species are distinguished.



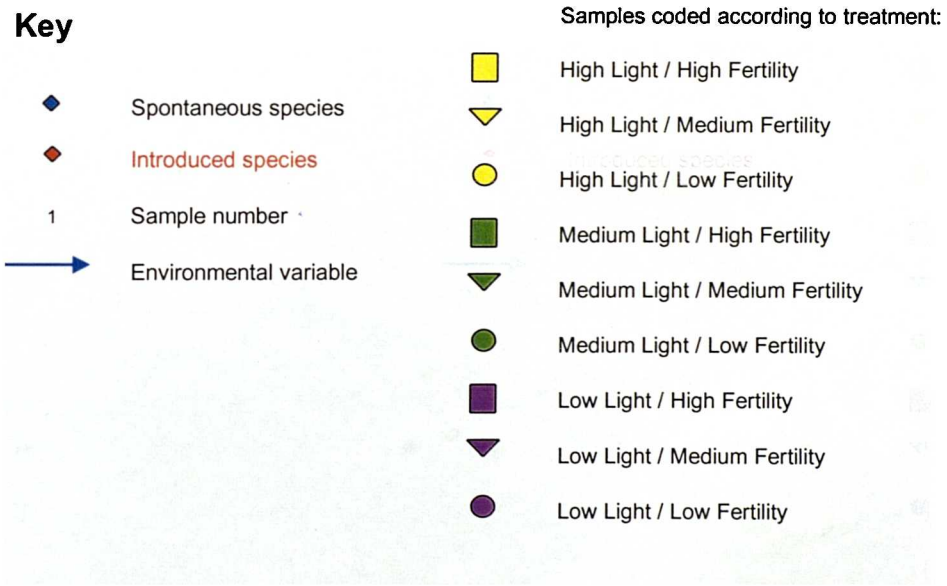


Figure 5.4 RDA Triplot of species, samples and environmental variables for the pre-harvest vegetation data of Experiment 3. This shows the environmental variables which have a significant influence on the development of the vegetation. Treatment and sample position effects are evident.

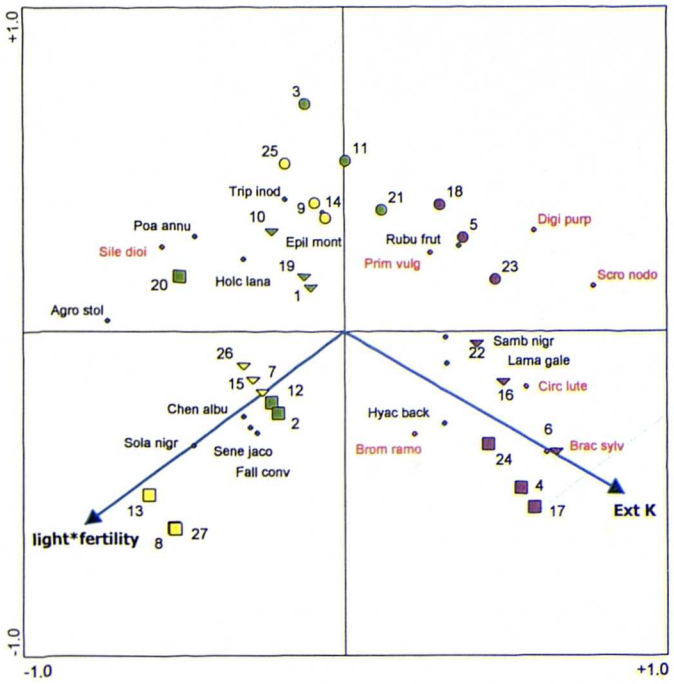


Figure 5.5 RDA triplot of species, samples and environmental variables for the pre-harvest vegetation data. This shows the environmental variables which have a significant influence on vegetation development, when the light and fertility treatment factors are combined as an interaction. Refer to Figure 5.4 for key.

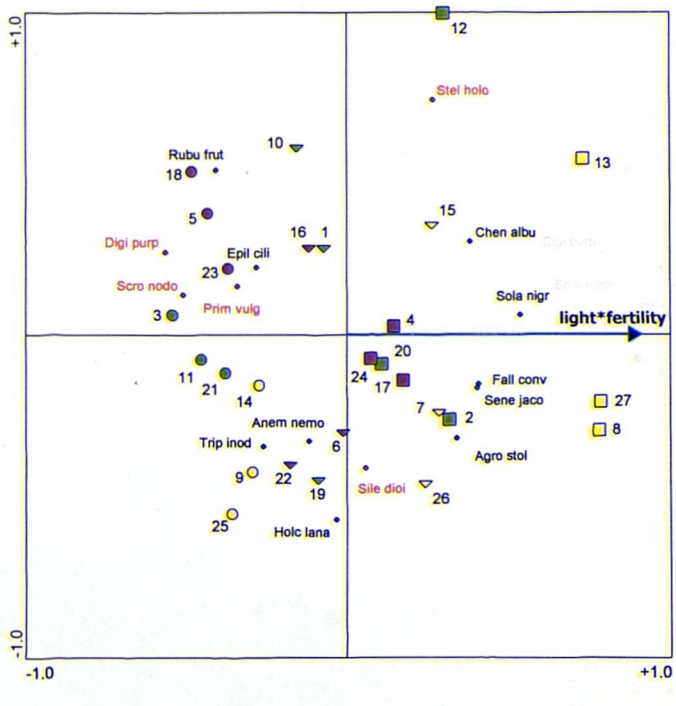


Figure 5.6 RDA triplot of species, samples and environmental variables for the pre-harvest vegetation data. In this model the light and fertility treatment factors have been combined as an interaction, and the potassium effect (Figure 5.5) has been partialed out, leaving only the treatment interaction significant. Refer to Figure 5.4 for key.

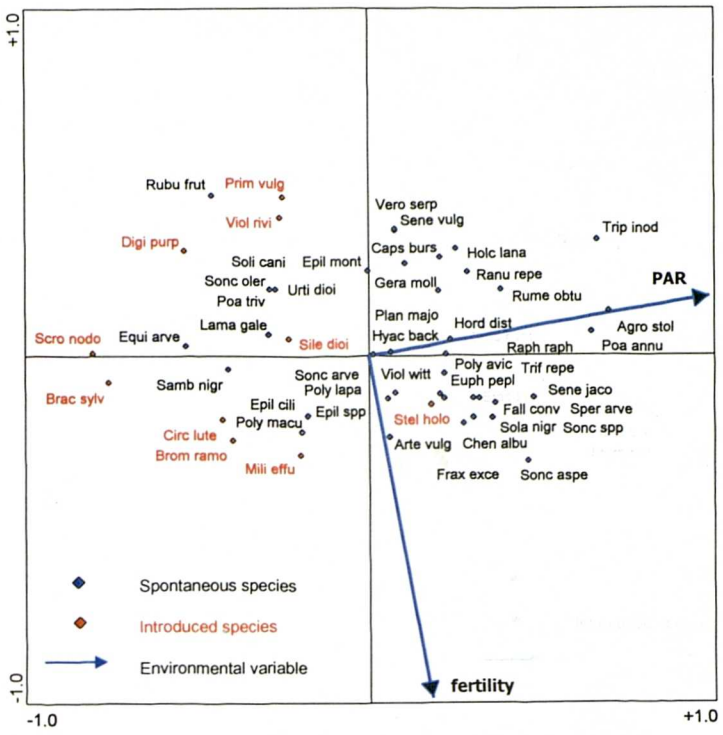


Figure 5.7 RDA Biplot of species and significant environmental variables for survey 2 vegetation data from Experiment 3. Introduced and spontaneous species are differentiated.

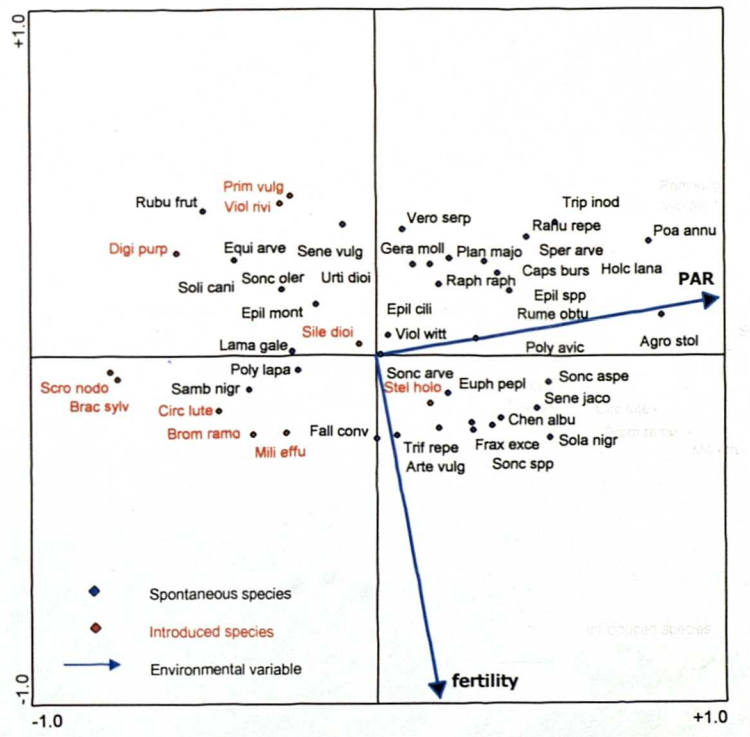


Figure 5.8 RDA Biplot of species and significant environmental variables for survey 3 vegetation data from Experiment 3. Introduced and spontaneous species are differentiated.

Abundance class	Light treatment 1 Low light	Light treatment 2 Medium light	Light treatment 3 High light
V	*Scrophularia nodosa* *Silene dioica*	*Scrophularia nodosa* *Silene dioica*	*Agrostis stolonifera* *Silene dioica*
IV	*Brachypodium sylvaticum* *Bromopsis ramosa* *Digitalis purpurea* *Rubus fruticosus* *Sambucus nigra*	*Agrostis stolonifera* *Digitalis purpurea* *Stellaria holostea*	*Holcus lanatus* *Solanum nigrum* *Stellaria holostea*
III	*Agrostis stolonifera* *Circaea lutetiana* *Holcus lanatus* *Solanum nigrum* *Stellaria holostea*	*Brachypodium sylvaticum* *Bromopsis ramosa* *Holcus lanatus* *Solanum nigrum*	*Brachypodium sylvaticum* *Epilobium ciliatum* *Scrophularia nodosa* *Tripleurospermum inodorum*
II	*Epilobium ciliatum* *Primula vulgaris* *Sonchus* spp. *Viola riviniana*	*Epilobium ciliatum* *Rubus fruticosus* *Sonchus* spp. *Tripleurospermum inodorum*	*Bromopsis ramosa* *Digitalis purpurea* *Rubus fruticosus* *Sonchus* spp.
I		*Circaea lutetiana* *Primula vulgaris* *Sambucus nigra* *Viola riviniana*	*Primula vulgaris* *Viola riviniana*

Table 5.4 Species abundance table for the three light treatments. The method by which these species were assigned to abundance classes is given in Section 5.2.5.3. Introduced species are shown in red.

Figure 5.9 Effect of light treatment on the mean biomass of introduced and spontaneous species per light treatment replicate. Letters denote significant differences between treatment means ($p < 0.05$): a, b, c for introduced species and a^1, b^1, c^1 for spontaneous species (Figures 5.9, 5.10, 5.13–5.18). Positive standard error bars are shown.

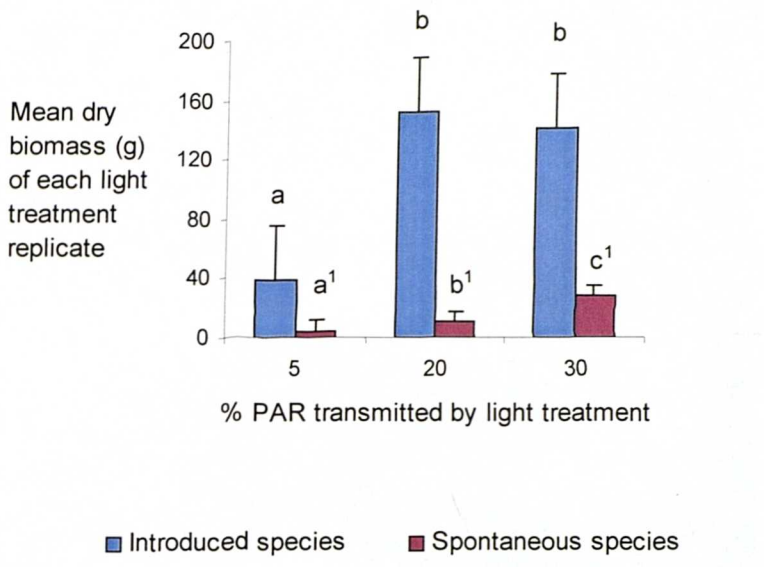


Figure 5.10 Effect of fertility treatment on the mean biomass of introduced and spontaneous species per fertility treatment replicate.

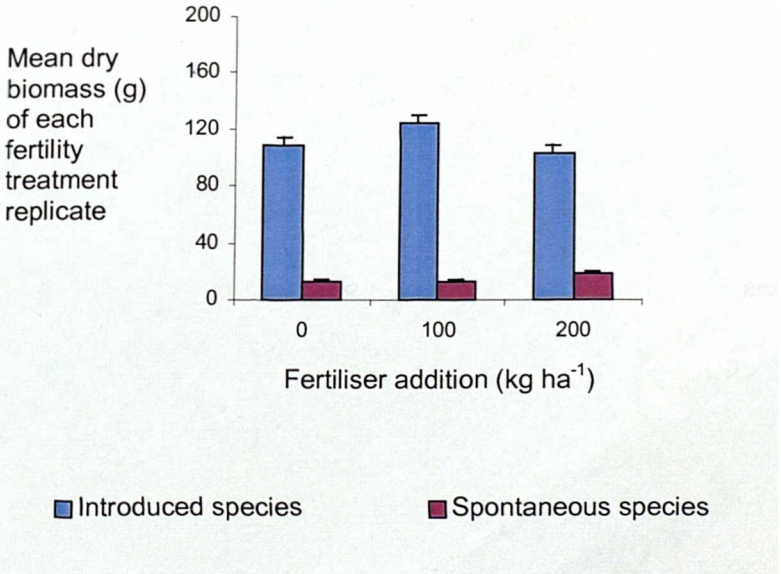


Figure 5.11 Effect of light treatment on mean weed biomass per light treatment replicate. Letters denote significant differences between treatment means ($p < 0.05$). Positive standard error bars are shown.

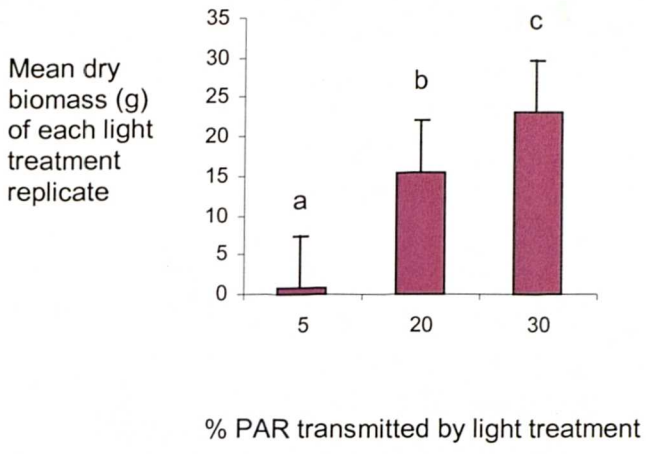


Figure 5.12 Effect of fertility treatment on mean weed biomass per fertility treatment replicate.

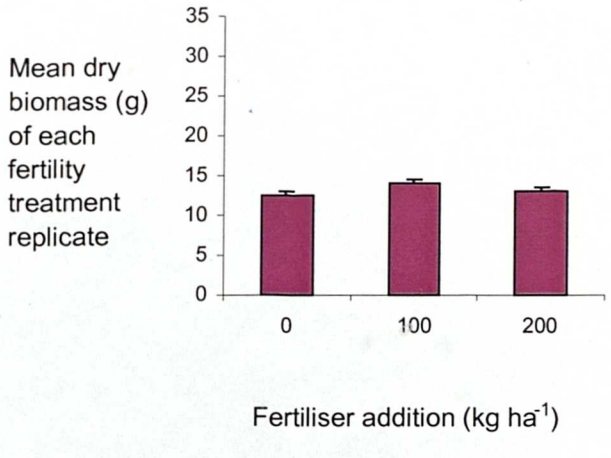


Figure 5.13 Effect of light treatment on mean densities of introduced and spontaneous species, per light treatment replicate, recorded in survey 1. Letters denote significant differences between treatment means ($p < 0.05$): a, b, c for introduced species and a^1, b^1, c^1 for spontaneous species (Figures 5.9, 5.10, 5.13–5.18). Positive standard error bars are shown.

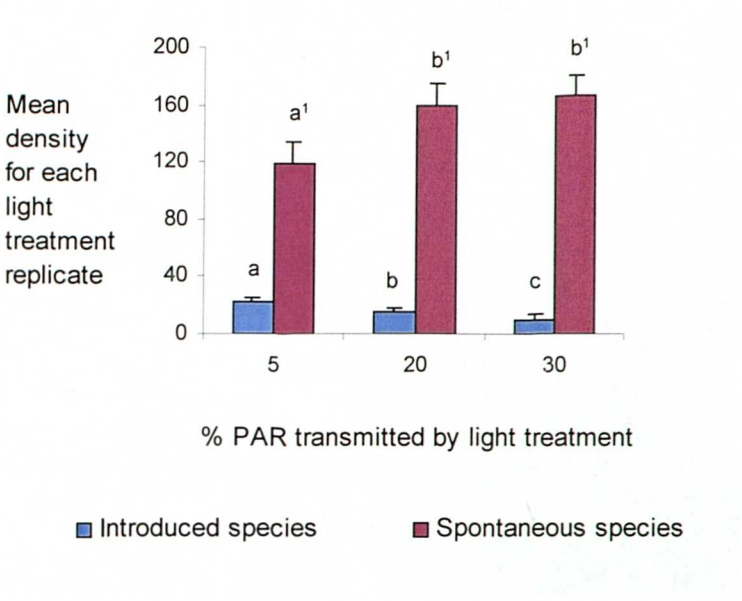


Figure 5.14 Effect of fertility treatment on mean densities of introduced and spontaneous species, per fertility treatment replicate, recorded in survey 1.

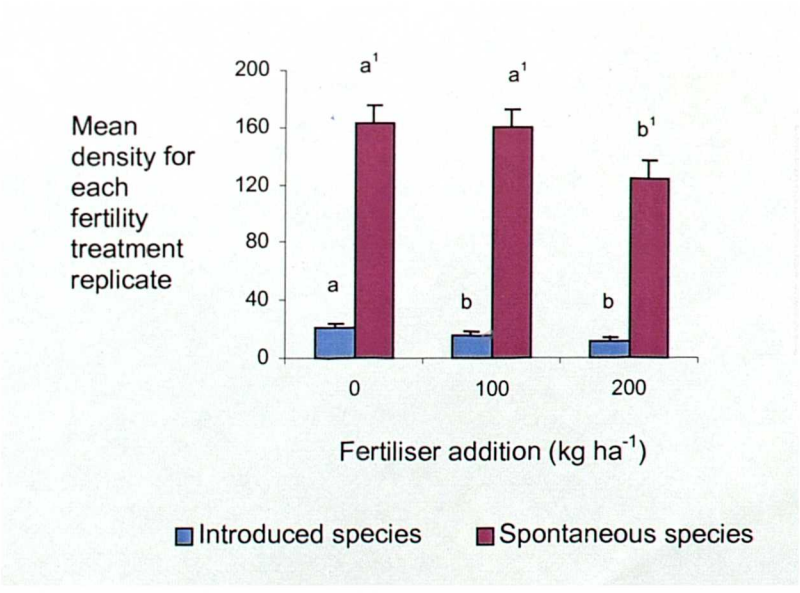


Figure 5.15 Effect of light treatment on mean densities of introduced and spontaneous species, per light treatment replicate, recorded in survey 2. Letters denote significant differences between treatment means ($p < 0.05$): a, b, c for introduced species and a^1, b^1, c^1 for spontaneous species (Figures 5.9, 5.10, 5.13-5.18). Positive standard error bars are shown.

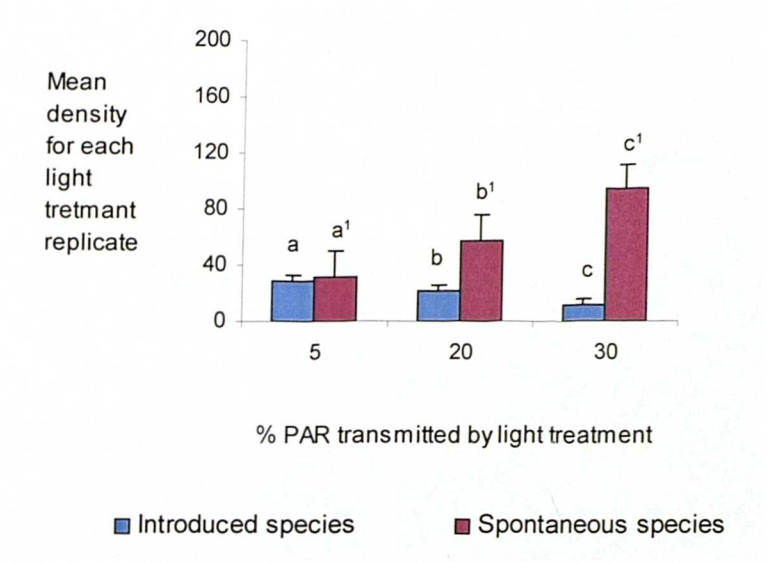


Figure 5.16 Effect of fertility treatment on mean densities of introduced and spontaneous species, per fertility treatment replicate, recorded in survey 2.

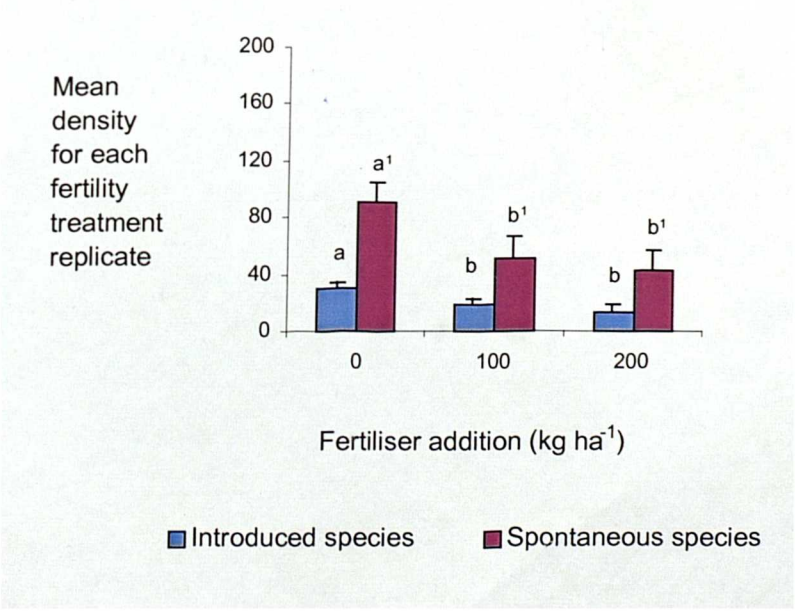


Figure 5.17 Effect of light treatment on mean densities of introduced and spontaneous species, per light treatment replicate, recorded in survey 3. Letters denote significant differences between treatment means ($p < 0.05$): a, b, c for introduced species and a^1, b^1, c^1 for spontaneous species (Figures 5.9, 5.10, 5.13–5.18). Positive standard error bars are shown.

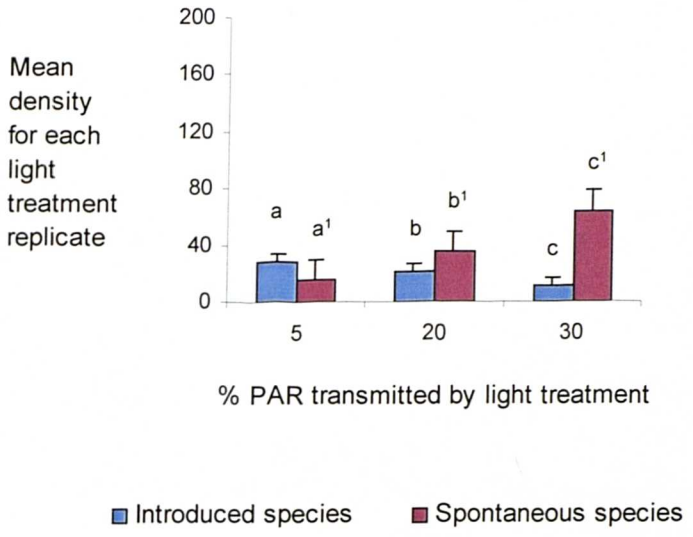


Figure 5.18 Effect of fertility treatment on mean densities of introduced and spontaneous species, per fertility treatment replicate, recorded in survey 3.

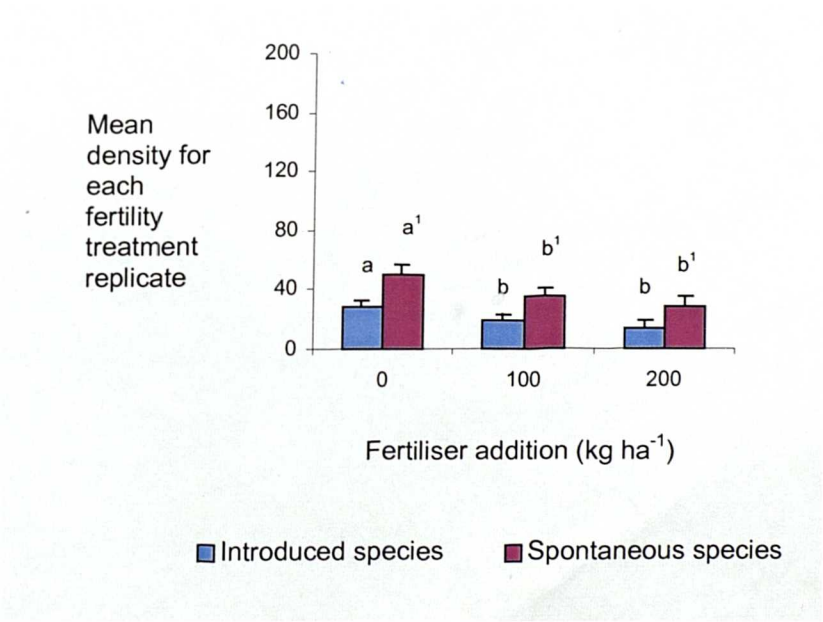


Figure 5.19 Effect of light treatment on mean densities of introduced species, per light treatment replicate, recorded in survey 4. Letters denote significant differences between treatment means ($p < 0.05$). Positive standard error bars are shown.

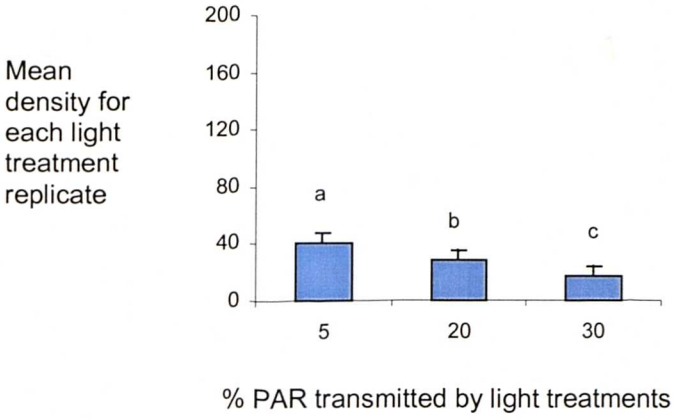


Figure 5.20 Effect of fertility treatment on mean densities of introduced species, per fertility treatment replicate, recorded in survey 4.

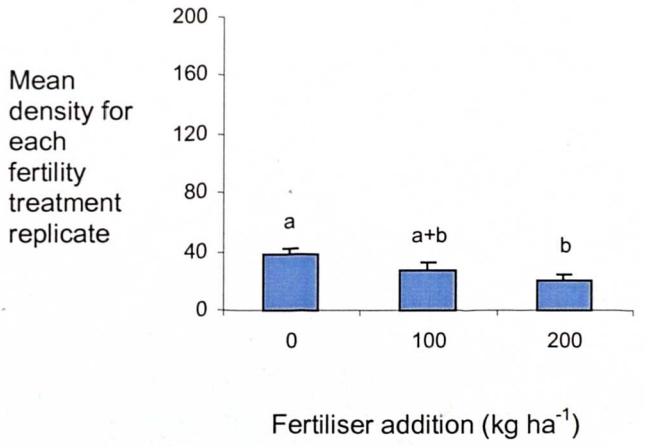


Figure 5.21 Significant interactions ($p < 0.05$) between light intensity and soil fertility on the mean density of introduced species in surveys a)1, b) 2 and c) 3. Positive and negative standard error bars are shown.

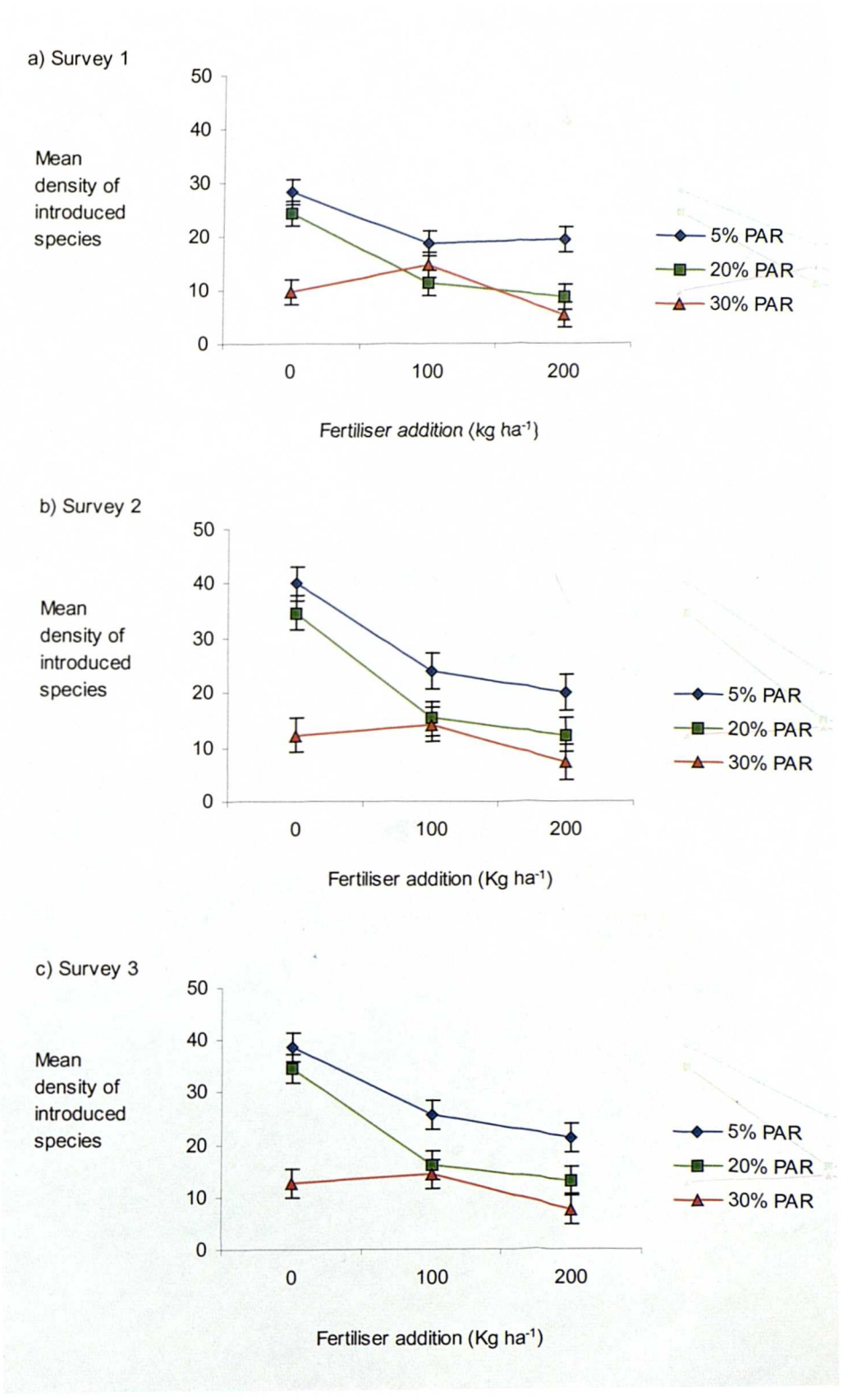


Figure 5.22 Effect of light treatment on mean recruitment of introduced species, per light treatment replicate, between surveys. Letters denote significant differences between treatment means ($p < 0.05$): a, b, c for Survey 1-2, a^1, b^1, c^1 for Survey 2-3 and a^2, b^2, c^2 for Survey 3-4 (Figures 5.22–5.23). Positive standard error bars are shown.

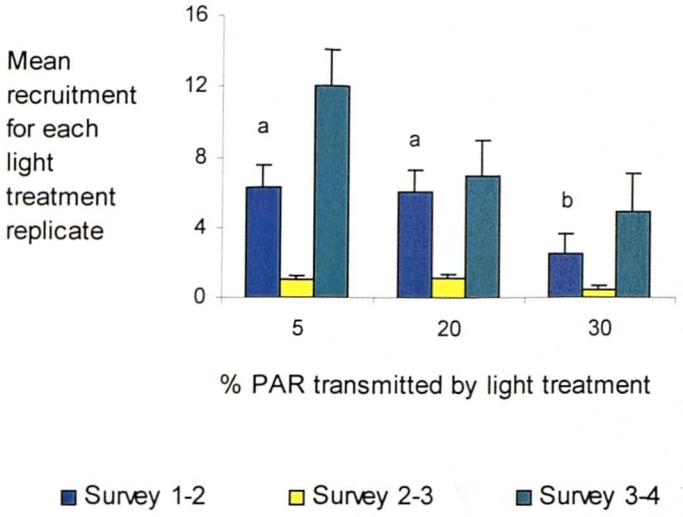


Figure 5.23 Effect of fertility treatment on mean recruitment of introduced species, per fertility treatment replicate, between surveys.

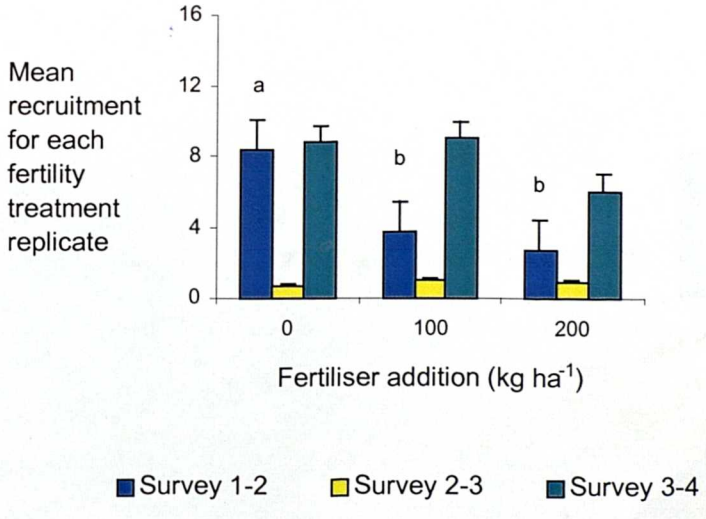


Figure 5.24 Effect of light treatment on mean densities of *Silene dioica*, per light treatment replicate, recorded in different surveys. Letters denote significant differences between treatment means ($p < 0.05$): a, b, c for Survey 1, a^1, b^1, c^1 for Survey 2, a^2, b^2, c^2 for Survey 3 and a^3, b^3, c^3 for Survey 4 (Figures 5.24–5.29). Positive standard error bars are shown.

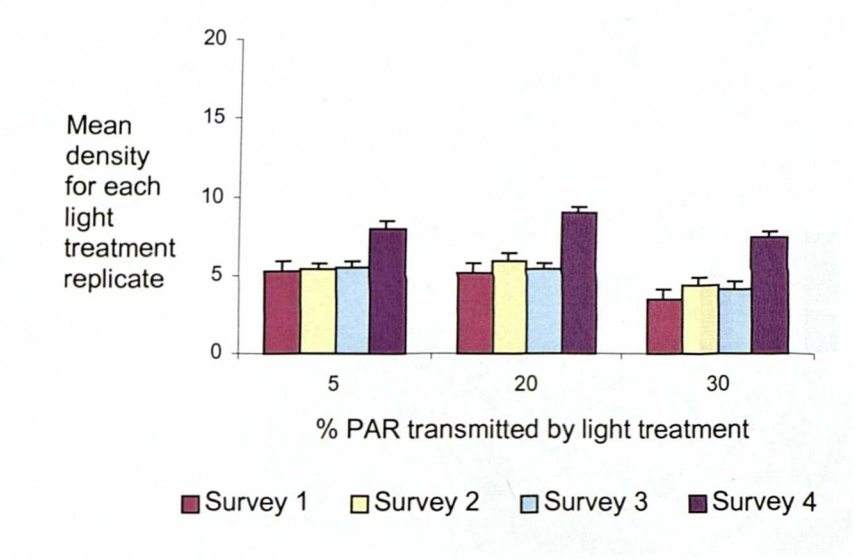


Figure 5.25 Effect of fertility treatment on mean densities of *Silene dioica*, per fertility treatment replicate, recorded in different surveys.

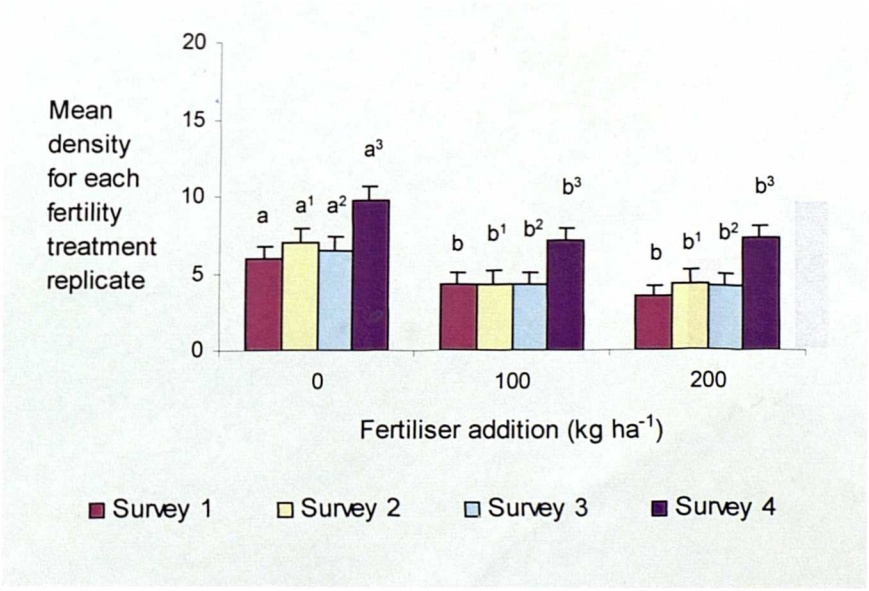


Figure 5.26 Effect of light treatment on mean densities of *Scrophularia nodosa*, per light treatment replicate, recorded in different surveys.

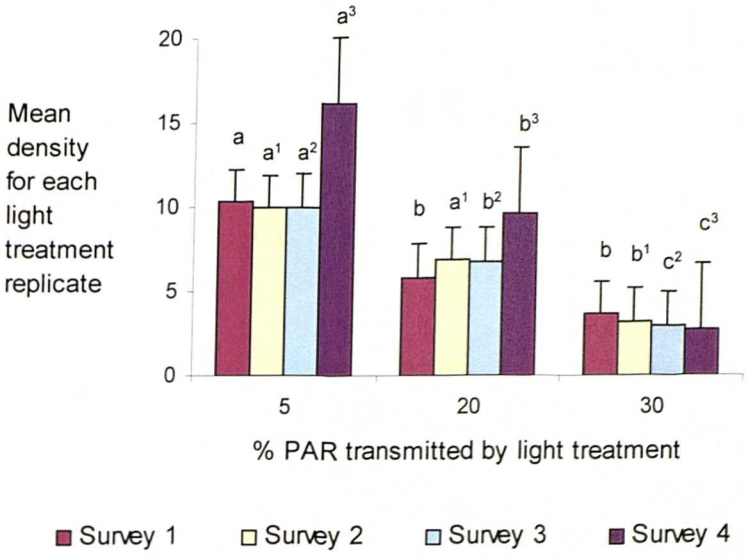


Figure 5.27 Effect of fertility treatment on mean densities of *Scrophularia nodosa*, per fertility treatment replicate, recorded in different surveys.

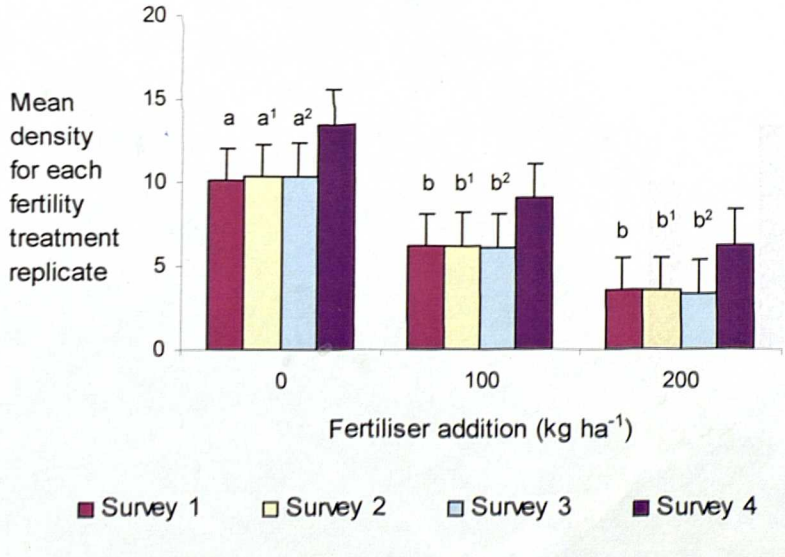


Figure 5.28 Effect of light treatment on mean densities of *Brachypodium sylvaticum*, per light treatment replicate, recorded in different surveys.

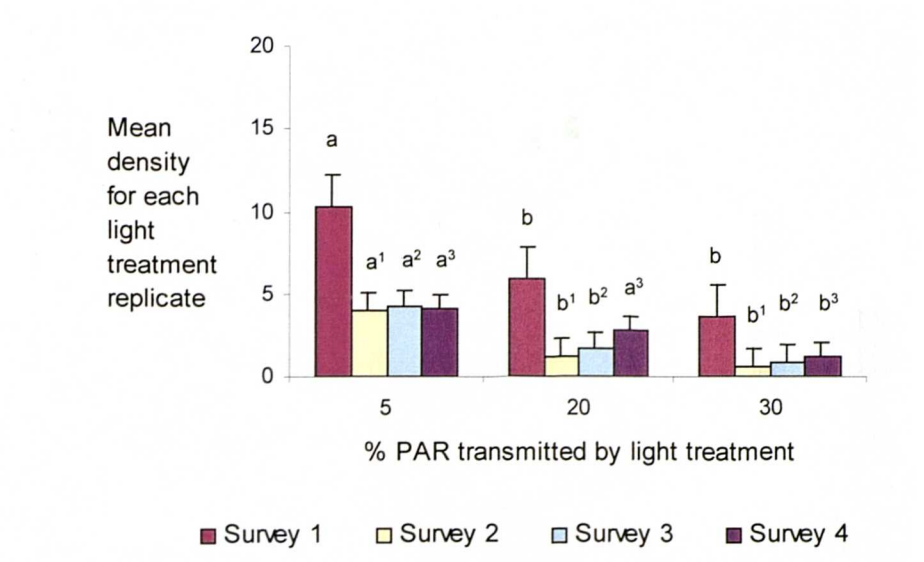
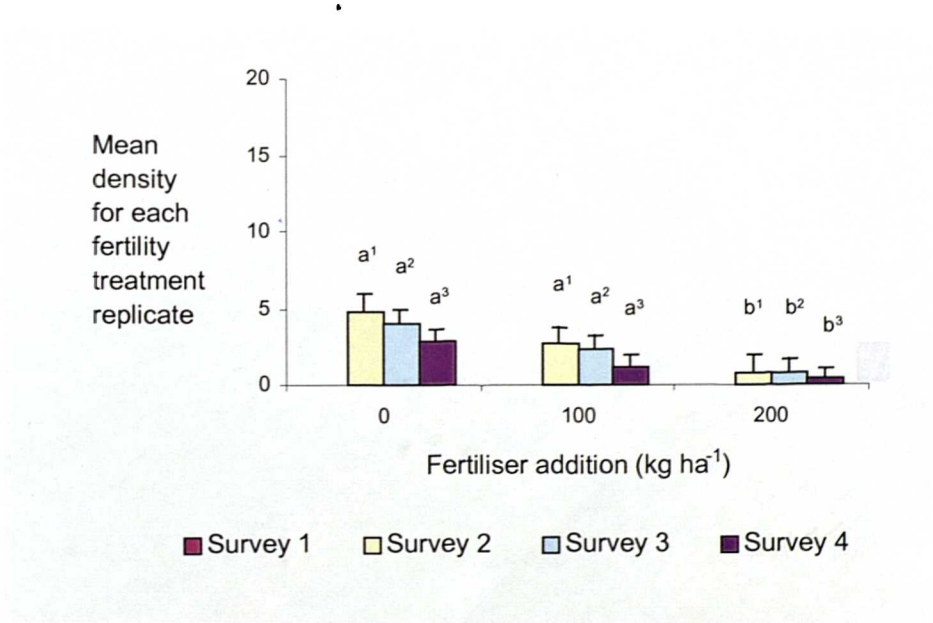


Figure 5.29 Effect of fertility treatment on mean densities of *Digitalis purpurea*, per fertility treatment replicate, recorded in different surveys.



Chapter 6: Discussion

6.1 Introduction

The central aims of the present investigation were to assess the importance of light intensity and soil fertility, singly and in combination and interaction, on field layer development in secondary woodlands with enhanced ground floras and in experimental ground flora communities. The objectives were to add to the methodology for ground flora enhancement and woodland habitat creation schemes and to contribute to the management of secondary woodlands to maximise representation of target ground flora communities. In this chapter, results from the entire experimental programme are compared and contrasted. The influence of environmental factors independent of the light climate or soil environment are also considered and compared across the experimental programme. The experimental findings are placed in the wider context of woodland and habitat creation research and are used to identify management implications and inform guidance for land managers. The limitations of the current study are summarised and recommendations made on further areas for research.

6.1.1 Summary of findings from the experimental programme

Experiment 1: The light manipulation experiment at the Wolverhampton Environment Centre.

- Woodland ground flora communities can be introduced into vigorous spontaneous secondary woodland communities without the use of a herbicide pre-treatment.
- The light climate was a major determinant of field layer development in both plantations.
- Thinning altered the light climate and affected ground flora response.
- Thinning and the associated disturbance altered establishment environments, but the relative importance of light and disturbance was unclear.
- Plot and plantation edge effects were maximised in the small stands of Experiment 1, which encouraged establishment of both introduced and spontaneous species. The limited window of thinning influence in small plots may aid early elimination of non-woodland species, but introductions are unlikely to persist at the woodland edge.

Treatment plot size and buffer zone size are important in the context of ground flora enhancement schemes.

- Bryophytes played an important role in niche microclimate amelioration in the Norway maple plantation.

- Soil fertility, as influenced by the nitrogen fixing capabilities of the Italian alder trees, produced the overriding relationship with the vegetation in this plantation.

- It was concluded that the canopy species in these monospecific plantations had the greatest influence on ground flora development. Summer light climate, i.e. dark phase, as influenced by canopy architecture in the Norway maple plantation and the augmented soil fertility in the Italian alder plantation, respectively produced the strongest correlations with the field layer vegetation.

Experiment 2: The soil fertility and light manipulation experiment at Nedge Hill.

- The larger plot size and 'whole wood' buffer zone largely overcame the edge effects evident in Experiment 1.

- The environmental effects of tree canopy species were diluted not only by the mixed broad-leaved species nature of the plantation at Nedge Hill, but also by slope effects.

- Background variation in environmental variables related to slope effects were a major determinant of field layer development. Litter cover was inversely proportional to soil mineralisable nitrogen and was associated with the secondary south-westerly slope. These variables were more closely associated with the field layer vegetation than the pH gradient, which was correlated with the main north-westerly slope.

- Whilst these background slope-related environmental variables largely determined niche space, thinning and fertilisation appeared to enhance the success of introduced species within available niches. However, the effects of fertilisation treatment on field layer vegetation were difficult to detect and to separate from the overriding background fertility effects.

- Soil fertility and light intensity interacted positively at the species level to enhance the establishment of *Campanula trachelium* and *Stellaria holostea*.

- Background soil fertility at Nedge Hill was believed to be close to optimum for ground flora enhancement. It was concluded that if soil fertility had provided an obstacle to successful establishment of introduced species, that it would have been impracticable to manipulate soil fertility in a direction or on a scale likely to ameliorate the situation.

Experiment 3: The soil fertility and light manipulation experiment at the Plant and Environment Research Unit.

- Light intensity was the most influential measured variable in the vegetation response of the experimental ground flora communities created in the controlled environment of the polytunnel.

- Soil fertility was negatively associated with the establishment success of the introduced species, but its influence was very much secondary to that of light intensity, and ceased to be significant when measured in its component parts.

- Soil fertility and light intensity acted singly, in combination and in interaction in affecting ground flora response at community and species levels. Soil fertility appeared to exert greatest influence before light became limiting, after which low light apparently negated the negative effects of soil fertility on diversity.

- The interaction between soil fertility and light intensity was complex, with different factors exerting influence on different parts of the community at different developmental stages. Low fertility and light levels were important for seedling recruitment of introduced species during establishment and early community development; light intensity appeared to be the controlling factor on the biomass parameters which represented late community development.

- Low light levels (5% of ambient PAR) favoured the success of the ground flora introductions, when in competition with arable weeds and vigorous non-woodland grasses.

- Soil fertility was negatively associated with the success of the ground flora introductions. Nevertheless under a high light regime (30% PAR), fertilisation equivalent to 100 kg ha^{-1} N:P:K compound agricultural fertiliser did not appear to have a detrimental effect on these species and apparently helped them to compete with spontaneous species.

6.2 The influence of light intensity on field layer development

There are several major comparisons that can be made between field Experiments 1 and 2. In terms of the light climate, the 'whole-wood' buffer zone of Experiment 2 largely eliminated the edge effects evident in Experiment 1. For example, there was no initial flush of non-woodland annual ruderal species in Experiment 2. Potential colonisation sources were further from the experimental area. Annual weeds are likely to be persistent in the seedbank; however, the seedbank in the longer-established plantation at Nedge Hill should have contained fewer non-woodland species than that at the Wolverhampton Environment Centre. This colonisation by non-woodland species is characteristic of increased irradiance following thinning and is consistent with findings from many studies (e.g. Reader and Bricker, 1994; Dzwonko, 2001). Experimental plots were larger in Experiment 2, which helped minimise plot edge effects and extended the window of treatment influence.

In both field Experiments 1 and 2, thinning the existing canopy cover by 50% enhanced the success of the ground flora species introductions, at both community and species levels. In *c.* 40 year old Canadian secondary broad-leaved forest dominated by *Quercus* species, Reader and Bricker (1994) found that only light thinning (i.e. 33% removal of tree basal-area from a 0.01 ha plot) was likely to be compatible with nature conservation management objectives. Thinning the canopy by 66%, or by 33% in larger plots, led to forest floor irradiance levels of more than 8% of incident light, which promoted invasion by non-woodland species and resulted in the development of a non-woodland ground flora. Annual non-woodland species are unlikely to provide a management problem and perennial non-woodland species are likely not to persist in the longer-term as the effects of thinning decline (Ford and Newbold, 1977; Kirby, 1988). It is the woodland species, such as *Digitalis purpurea* and *Geum urbanum*, that are best adapted to persist throughout the changing light climate that occurs during the forest cycle (van Baalen and Prins, 1983; Pons, 1977b, respectively). Possibly the findings of Reader and Bricker (1994) suggest that other environmental variables might have been tipping the competitive balance between the woodland and non-woodland species and limiting the maximum infiltration at which woodland species were successful.

In the present study thinning was undertaken from different and varied canopy starting points, so the amount of PAR reaching the field layer (expressed as a percentage of ambient levels) was used as an absolute measure of the light climate and of the effects of

the thinning treatment on the light climate. Table 6.1 shows the PAR ranges most associated with successful establishment of introduced species across the experimental programme, which were mostly associated with thinned plots in the field experiments. These 'optimal ranges' of dark and light phase PAR are surprisingly consistent across the experimental programme, despite large differences in canopy type. The experiments suggest that an average range of 5-20% summer infiltration of PAR should be aimed for in thinned areas. The median of 12.5% is probably a good point to aim for if other site conditions are ideal for ground flora introductions. Canopy thinning to produce such a range of summer light levels should equate to a favourable winter light climate, with average light phase PAR levels of 60-80%. Close to the median of 70% is probably ideal. To put these PAR ranges into context, Mitchell (1992) said that light transmission under a full canopy could be reduced from 50% during the woodland light phase to 2.5% in the woodland dark phase. The relatively young secondary woodlands in the current research clearly represent a more open and therefore lighter starting point than Mitchell's (1992) example. At PAR levels greater than about 20% of ambient levels, the introduced species can become established, but are likely to face greater competition from non-woodland spontaneous species, as in the Italian alder plantation and the high light treatment (30% PAR) of Experiment 3.

Table 6.1 Between-experiment comparison of estimated optimal ranges for the light climate. Variables considered major determinants of ground flora development are highlighted in bold. (NB. The artificial light climates in Experiment 3 were constant throughout the experiment; i.e. no attempt was made to mimic the woodland light phase).

Environmental variable	Experiment 1 Norway maple	Experiment1 Italian alder	Experiment 2	Experiment 3
Dark phase PAR (%)	**10-20**	18-28	**8-14**	**5-20**
Light phase PAR (%)	68-78	**63-73**	**62-70**	n.a.

In Experiment 3, the lowest light treatment, transmitting 5% PAR, was the most successful in terms of favouring introduced species (apart from *Silene dioica*) over the spontaneous 'arable weed flora'. This perhaps indicates that summer light climates at the lower end of the 'optimum PAR range' are preferable when conditions, in terms of competition, are less than ideal for ground flora introductions. In Experiment 3, the high level of competition from the arable weed flora created less than optimal establishment

conditions. The comparatively uniform and stable environmental conditions within the polytunnel would have probably been more favourable to the introduced species and their spontaneous competitors compared with the variable conditions of the field experiments. Also seed and seedling predation would probably have been higher in the field. The existence of an established spontaneous vegetation prior to ground flora species introductions in the field experiments would further limit available niche space compared to that in Experiment 3.

Thinning also influences variables other than irradiance reaching the woodland floor. Increased light intensity due to thinning also causes changes in light quality, with an increase in the red to far-red ratio (Endler, 1993), which influences the phenology of woodland ground flora plants (e.g. Fitter and Ashmore, 1974; Mitchell and Woodward, 1988). The present study uses light intensity (in the form of PAR) reaching the field layer as an indicator or proxy measure for other light climate variables (Section 6.7). Thinning also influences non-light variables; for example, the disturbance associated with silvicultural operations affects surface parameters, such as temperature and litter cover (Sections 6.3 and 6.5, respectively), which will influence nutrient turnover.

Of the environmental variables measured in field Experiments 1 and 2, dark phase PAR was generally most correlated with the species distribution of the field layer vegetation (except in the Italian alder plantation of Experiment 1, where light phase PAR appeared more important). The loss of trees to 'wind-blow' in the thinned Italian alder plots accounts for the higher average summer light infiltration in this experiment (Table 6.1). Although the response of the introduced species does not appear to have been adversely affected by the increased irradiance due to tree loss, it may account for the greater influence of the light phase light climate on the vegetation as dark phase PAR becomes sub-optimal. Light phase PAR appeared to have been relatively unaffected by the tree loss in the Italian alder plantation. Light phase PAR is far less dependent on tree canopy characteristics than dark phase PAR and is therefore likely to be more consistent across sites. Nevertheless the dark phase PAR optimal ranges between the monospecific Norway maple plantation of Experiment 1 and the mixed plantation of Experiment 2 are comparable. Light phase PAR was significantly correlated with plant distribution in Experiment 2, but was less important than dark phase PAR. This aspect of the light climate may be more significant in large woodlands, where plots are not subjected to side light, as they were in Experiment 1. Light phase PAR was more positively associated

with the introduced species in Experiment 2 than it was in the Italian alder plantation of Experiment 1. Light phase PAR may become more important with later community development, when slow establishing vernal species, such as *Hyacinthoides non-scripta,* have made an impact on the vegetation.

The distribution, height and cover of the canopy plants largely determine the understorey light climate (Martens *et al.*, 2000). The contrast in vertical light gradients, the importance of which is acknowledged by Grime and Jeffrey (1965), that would be expected to occur between the complex vertical structure of Nedge Hill (incorporating a shrub layer) and the relatively simple stand structures at the Wolverhampton Environment Centre may not be a major determinant of ground flora development. The relative consistency of light climates across the varied canopies of the field experiments suggests perhaps that canopy architecture due to tree species (including vertical layering) does not exert so great an influence on light regime as originally hypothesised.

Although most of the introduced species grew throughout the full range of light intensities found in the experimental programme (Experiment 3 illustrates this well), higher levels of dark phase PAR (up to about 20%) favoured the success of these species in the field. For example, *Primula vulgaris* occurred at greater densities in the thinned plots in the Norway maple plantation of Experiment 1 and in Experiment 2. The fecundity of this species is reported to be positively correlated with light (Valverde and Silvertown, 1995). Sun and shade adaptations allow species like *Silene dioica* (Willmot and Moore, 1973) to survive in the changing light climate of the forest cycle. The light regime into which these species are introduced may however be critical to their future survival. Pitelka and Curtis (1986) found that establishment light climate dictated whether *Aster acuminatus* seedlings developed into sun or shade plants, and Hutchinson (1967) found that light climate at establishment influenced plant ability to tolerate prolonged darkness. Whilst introductions in the field experiments responded positively to high summer irradiance levels (up to 20% of ambient PAR), this is in stark contrast to the 5% PAR infiltration which favoured introduced species in the intensely competitive environment of the experimental communities in Experiment 3.

6.3 The influence of soil fertility on field layer development

Experiment 1 was established on a relatively artificial and infertile substrate which provided an analogue for urban soils, whereas Experiment 2 was established on a more developed, fertile, ex-agricultural soil (Section 2.2). The plantation at Nedge Hill is not only, in terms of soil and vegetation development, closer to the target ancient semi-natural woodland (Section 1.4.1) than the Wolverhampton Environment Centre plantations, but it provides a reasonable analogue for farm woodlands (Francis *et al.*, 1996). It was thought that the relatively free-draining properties of soils at Nedge Hill (Ragg *et al.*, 1984) might mitigate the effects of high soil fertility. Although baseline soil fertility was not measured directly, the evidence from the field experiments suggests that the fertility treatments had complex effects on soil fertility.

The relative evenness of the visual treatment effect evident in the soil nutrient contour maps (Figures 4.4–4.6) from Experiment 2 indicates a relatively uniform fertility baseline at Nedge Hill. However, the field layer was clearly responding to spatial variation in aspects of background soil fertility, as opposed to variation in the soil environment induced by fertilisation treatment. Comparisons between the nutrient contour maps (Figures 4.4–4.6) and the density distribution of introduced species in the second year (Figure 4.13) allow the prediction of optimum ranges for the soil macronutrients in terms of maximising the response of introduced species. Table 6.2 shows these ranges and presents those from the rest of the experimental programme for comparison. These soil nutrient ranges portray an indication of the soil conditions which achieved positive results, but they do not have any statistical basis.

Table 6.2 Between-experiment comparison of estimated optimal ranges for soil fertility variables. Variables considered major determinants of ground flora development are highlighted in bold.

Environmental variable	Experiment 1 Norway maple	Experiment 1 Italian alder	Experiment 2	Experiment 3
pH	**5.2-5.5**	5.5-6.2	5.5-6.1	4.9-5.6
Soil organic matter (%)	7	8-9	5-7	8-15
Mineralisable N (mg kg^{-1})	46-62	**64-80**	**75-105**	15-74
Extractable P (mg kg^{-1})	20-35	**8-22**	22-30	15-59
Extractable K (mg kg^{-1})	95-120	**115-155**	140-190	**50-300**

Various aspects of soil fertility were correlated with variation in the field layer vegetation in all of the experiments. Only in the Italian alder stand of Experiment 1 was more than one factor significant. Here, the nitrogen fixing ability of the alders raised soil fertility in terms of mineralisable nitrogen and extractable potassium. This appeared to have had a largely negative response on the introduced species, by putting the aggressive spontaneous species at a competitive advantage. However, the optimal range of mineralisable nitrogen at Nedge Hill is greater than in the Italian alder plantation and was positively associated with the introduced species. Perhaps the increased summer light stress (Table 6.1), patchy niche space (Section 6.5), distance to weed-colonisation sources and comparatively undisturbed soil seedbank at Nedge Hill combine to allow the introduced species to benefit from enhanced nitrogen uptake, without the threat of major competition from aggressive and / or non-woodland species. It is also possible that the negative effects, on the development of the introduced ground flora, of raised soil nitrogen and potassium in the Italian alder plantation could be mitigated in places by phosphorus limitation (Table 6.2). Increased mineralisable nitrogen has been correlated with higher community diversity (Marrs, *et al.*, 1991), who explained the correlation by the enhanced nutrient cycling which develops with succession over time. Mineralisable nitrogen may provide a proxy measure for the development and activity of soil micro-biota, the quantification of which was beyond the scope of this research. Perhaps the level of mineralisable nitrogen at Nedge Hill simply reflects a more advanced succession and development of nutrient cycling systems (Packham *et al.*, 1992).

The increased levels of soil phosphorus and potassium in Experiment 3, one year after fertilisation treatment, contrasts with the apparent decrease in extractable phosphorus associated with fertilisation in field Experiment 2, where the record of fertiliser application being so clearly correlated with nutrient depletion is unusual and unexpected. The peat component of the compost in Experiment 3 aided nutrient retention, with apparently little loss via leaching. By contrast, the relatively free-draining soils at Nedge Hill would have been prone to nutrient leaching and the surface disturbance caused by the fertilisation treatment may have exacerbated this process.

Fertilisation at Nedge Hill may also have enhanced nutrient depletion by the ground flora plants, although there is no direct evidence to support this supposition. The most obvious difference between Experiments 2 and 3 is the presence of a tree canopy in Experiment 2. The potential for tree nutrient uptake is greater than that of the field layer plants and

would appear to be the most likely cause of nutrient depletion. However, fertility depletion of soil phosphorus and potassium by ground flora plants was demonstrated in Experiment 3 where light was not limiting (i.e. in the two higher light treatments transmitting 20% and 30% PAR, respectively). There was no apparent correlation between the phosphorus depletion effects of fertilisation at Nedge Hill and plant distribution in the field layer. Disturbance and fertilisation may enhance nutrient losses via leaching (Persson and Wiren, 1986). Fertilisation can stimulate plant uptake of cations from deep in the soil profile (Turner and Lambert, 1986). Due to their root architecture trees are generally more able to exploit nutrients deeper in the soil profile than the field layer plants, so this may be a canopy rather than a field layer effect. The stimulation of deep-soil plant cation uptake is regarded as long-term (Turner and Lambert, 1986) and is perhaps more likely to be a result of pre-plantation agricultural fertiliser applications, at Nedge Hill, than a single and relatively recent experimental treatment. If the soluble phosphate pool is small (Allen *et al.*, 1989) plant uptake can lead to localised depletion (Rowell, 1994). In both Experiments 2 and 3 fertilisation influences the spatial distribution of available soil nutrients. However, it is light which apparently controls nutrient uptake in Experiment 3 while aspects of background fertility unaffected by fertilisation treatment, together with the light climate, appear to determine nutrient uptake in Experiment 2.

No detectable effect of fertility treatment was found on soil mineralisable nitrogen in the experimental programme. The limited soil sampling programme undertaken in this research does not allow prediction of the fate of this mobile macronutrient. Chang *et al.* (1997) found that inorganic nitrogen fertiliser was immobilised within hours of application by microbes in the woodland humus layer and that this nitrogen had little future mineralisation potential. This immobilisation occurred in a system with a large soil pool of mineral nitrogen, an unknown quantity in the current research. While mineralisable nitrogen was unaffected by fertility treatment, it was apparently influenced by thinning in the Norway maple plantation of Experiment 1. Thinning allows increased irradiance to reach the woodland floor, raising soil surface temperatures and enhancing the activity of the soil micro-biota. These effects, coupled with the associated disturbance and aeration of the litter and humic layers, as well as additional material being made available for decomposition, raises mineralisation potential. Kim *et al.* (1995) found that thinning only 25% of a northern red oak canopy in Michigan increased nitrogen mineralisation. Silvicultural treatment did not appear to influence other aspects

of soil fertility, except for soil organic matter in Experiment 1 (Section 6.5). Variations in mineralisable nitrogen levels were related to environmental variables other than those representing the light climate or soil environment (Section 6.5).

Although the introduced species were differently correlated with variations in soil fertility, most species grew well across the range of soil conditions in the experimental programme (Table 6.2). This supports the assertions of Fitter and Setters (1988), who found that six species of *Viola* showed considerable phenotypic plasticity in their wide range of phosphorus and potassium allocation patterns. Slade and Causton (1979) showed that *Silene dioica* and *Milium effusum* could germinate over a wide variety of nutrient conditions. Throughout the present experimental programme the introduced grasses, *Brachypodium sylvaticum, Bromopsis ramosa* and *Milium effusum*, plus *Stellaria holostea* and *Viola riviniana,* responded positively to higher nutrient levels, supporting the findings of Cohn (1994) and Lawley (1998). Pregitzer and Barnes (1982) found *Viola* species to be indicative of high total nitrogen levels and soil pH. However, *Viola riviniana* (the species introduced in the current research) failed to respond positively to nutrient-rich patches in an autecological study investigating species response to heterogeneous nutrient resources (Farley and Fitter, 1999b).

None of the optimal ranges of soil conditions measured in the experimental programme (Table 6.2) encompass extremes in the soil chemical environment which are likely to be detrimental to field layer diversity (Quist, 1995). Localised spatial variation in aspects of soil fertility can influence the intra-site heterogeneity of the vegetation response (e.g. Fitter and Setters, 1988). It is believed that background soil fertility at Nedge Hill was relatively uniform and fairly close to optimum for ground flora introductions. By contrast, soil conditions at the Wolverhampton Environment Centre were slightly more impoverished, but again not extreme. The exception to this was the relatively high level of available soil phosphorus in the Norway maple plantation. Reasons for this can only be speculated, as the detailed management history of the Wolverhampton Environment Centre is not known. From the present studies it is not clear which aspects of fertility are generally most important, as different aspects of soil fertility were significant in different experiments, although collectively fertility generally played a role secondary to light.

It is difficult to put the soil fertility results of the experimental programme into the wider context for several reasons. The variables measured, the chemical analyses used to measure them and the units that they are expressed in are not directly comparable with many studies in the literature. There are no comparable studies investigating the effects of woodland soil fertility on ground flora development. However, work on grassland habitat creation and community response, carried out within the University of Wolverhampton Habitat Creation and Vegetation Ecology Research Group, is comparable and can be used to provide some context to the results of the current study.

High residual soil fertility is traditionally considered a problem in habitat creation or restoration schemes (Cohn, 1994). In grassland creation schemes high levels of available phosphorus are believed to be the greatest obstacle to diversity (Gough and Marrs, 1990a,b; Marrs, 1993). The results from the current experimental programme are well below the recommended upper limit for extractable phosphorus which is likely to support a species-rich sward (< 70 mg kg^{-1}) (McCrea *et al.*, 2001b). However, Defra's (Department for Environment, Food and Rural Affairs) current guidance for acceptance of sites into Agri-environment schemes for arable reversion to a species-rich sward is that soil extractable phosphorus should be < 15 mg kg^{-1} (internal guidance note). The optimal ranges for ground flora enhancement in this study (Table 6.2) are well in excess of this value. However, Kirby (1997) suggested that woodland ground flora is more resilient to increases in soil fertility than grassland vegetation, as increasing nitrogen from atmospheric deposition in Wytham Woods caused no change in the Ellenberg nitrogen values of the ground flora vegetation during an 18 year period. This may be because ancient semi-natural woodlands like Wytham have a relatively undisturbed soil seedbank. In ancient woodlands germination niches, created through storm damage or management, are less likely to be prone to invasion by non-woodland species than either recent secondary woodlands or grasslands.

Vaz (2001) found that high levels of extractable potassium (> 300 mg kg^{-1}) were correlated with a decline in grassland diversity. The optimal ranges from the experimental programme (Table 6.2) fall below this postulated maximum. There are few recommendations in the literature for habitat creation and levels of mineralisable nitrogen. Ash *et al.* (1992) recommend that species-rich grassland creation be undertaken on infertile substrates and defined these as having < 2 μg g^{-1} mineralisable nitrogen, with 2-20 μg g^{-1} being intermediate and having some potential depending on other soil factors.

McCrea (1999) and Vaz (2001) found a humpback relationship, where community diversity is highest at intermediate levels of productivity (Grime, 1979), between mineralisable nitrogen and diversity in grasslands (created and semi-natural) and concluded that moderately species-rich swards could be created across a mineralisable nitrogen range of 10-100 mg kg^{-1}. This accords with the optimal ranges for ground flora enhancement found in the experimental programme (Table 6.2).

Soil pH and organic matter were not strongly correlated with ground flora development in the experimental programme (Table 6.2). Vaz (2001) found that while intra-site variation in plant communities was linked to pH in grassland, there was no direct association with diversity; similarly soil organic matter alone had no direct relationship with plant distribution. It is considered that the indirect influence of pH on nutrient availability (e.g. Luwe, 1995) is likely to override direct effects on plant distribution. Only the ground flora in the Norway maple plantation of Experiment 1 showed a direct relationship with soil pH. Generally the influence of soil pH on ground flora development may be more important in the long-term, as pH decreases with succession (Harmer *et al.*, 2001; Verheyen and Hermy, 2001). The role of soil organic matter is perhaps best discussed in conjunction with that of litter, with which it is closely linked (Section 6.5). Vaz (2001) found that the negative impacts of soil fertility could be offset in grassland ecosystems by high soil moisture, or water stress, which was not measured in the current research. In woodlands, it is likely that the additional, and probably overriding stress of shade from the canopy, will negate the effects of excessive soil fertility to a greater extent in this habitat (Packham *et al.*, 1992).

6.4 The influence of light and soil fertility in combination and in interaction on field layer development

The influence of light and soil fertility in combination and in interaction on field layer development was investigated in Experiments 2 and 3, and was statistically evident in the density response of the introduced species in both experiments. At first inspection, the results of the field experiments appear different from those of the polytunnel experiment. In the field the introduced species appeared to respond positively to both high light and fertility, whilst in the artificial ground flora communities, low light and fertility appeared to most favour target species. One of the obvious differences between the two experiments was the presence of a vigorous spontaneous vegetation in Experiment 3, which although present in Experiment 2, was far less concentrated and composed of

fewer non-woodland species. The field results accord with those of Braziotis and Papanastasis (1995), whose *Dactylis glomerata* under-sward responded positively to high light and fertility in a pine plantation. However, this non-woodland grass might be more expected to behave in this way than the woodland herbs introduced in the present experimental programme. Peterson and Philipp (2001) speculate that unfavourable soil, light and surface conditions (Section 6.5) caused localised extinctions in an introduced woodland ground flora. It must be concluded that the ranges of soil fertility and light climate generated in the field experiments were not unfavourable to the ground flora introductions within the context of competition from the prevailing spontaneous vegetation. However, in the artificial ground flora communities, although the target species all germinated across the range of soil and light conditions supplied by the experiment, they were out-competed by the spontaneous arable weed flora at higher levels of light and fertility. The progressive weakening of the interaction between soil fertility and light intensity on the density of the introduced species in Experiment 3 emphasises the importance of the establishment environment, as predicted by Cohn (1994).

The main difference in the light and fertility conditions provided in Experiment 3, compared to those prevailing in the field experiments, was the absence of a simulated woodland light phase. The light climate in Experiment 3 was constant at dark phase levels throughout the year. It might have been expected that this would favour the response of the truly shade-tolerant species like *Circaea lutetiana* and not that of the vernal sun plants like *Hyacinthoides non-scripta*. *Circaea lutetiana* was a prominent feature of the low light treatment in Experiment 3, whereas its establishment in the field was poor. However, the phenology of *Circaea lutetiana* dictates that it is not actively growing during the woodland light phase meaning that it would be unable to benefit from reduced competition in the field at this time. Unfortunately, the duration of Experiment 3 was too short to properly monitor the slow-establishing *Hyacinthoides non-scripta*.

Light effects on nutrient uptake by ground flora plants (both introduced and spontaneous) appeared to be paramount. In Experiment 3 there was some evidence that extractable potassium was positively associated with the introduced species (with the exception of *Silene dioica*), but the effect appeared to be negatively correlated with the light induced nutrient depletion effect (also evident in the extractable phosphorus results). Light stress in the lowest light treatment (5% PAR) of Experiment 3 severely limited the ability of

ground flora plants to utilise soil nutrients, which were depleted only at the two higher light levels (20% and 30% PAR transmission). The inability of the non-woodland plants to fully utilise soil nutrients under 5% PAR allowed niche space to become dominated by the introduced shade-tolerant woodland species.

The results of autecological studies on the response of woodland herbs to variations in light climate and soil fertility have common themes, from which insight into the nature of the interaction can be gained. Species which respond positively to additional nutrients do so at different and sometimes multiple points on the irradiance spectrum (e.g. Blackman and Rutter, 1947, 1948; Pigott and Taylor, 1964; Pigott, 1971; Peace and Grubb, 1982). In Experiment 3 a positive community response to nutrient uptake and depletion was only observed where light was not limiting, in the two higher light treatments, transmitting 20% and 30% of ambient PAR. However, if nutrients are limiting then minimum light requirements can increase in line with the nutrient stress (Ellenberg, 1988). There was no direct evidence to suggest that the hypothesised nitrogen limitation across Experiment 3 (Section 5.3.3) raised the minimum light requirements of the introduced species. Cohn (1994) showed that the target species *Silene dioica, Circaea lutetiana* and *Viola riviniana* all respond positively to nutrient additions when light was limiting, and to irradiance increase when mineral nutrient supply was limiting. The exception was *Circaea lutetiana,* which did not show a significant increase in the latter situation within the time scale of the experiment.

The results of Experiment 3 were obscured by the fungal attack and premature die back of *Silene dioica* in the lowest light treatment. The behaviour of individual species in competition with other target species and vigorous spontaneous vegetation is evident from the results of Experiment 3, and for this reason it is believed that the experiment perhaps went some way towards bridging the gap between autecological and field studies. For example, *Silene dioica* exhibited a negative density relationship with soil fertility and a positive relationship between biomass and light intensity. This could be explained as a niche colonisation *vs.* consolidation strategy. At low levels of fertility niche colonisation is maximised by increased seedling production, whereas at high light intensities established plants maximise leaf area for photosynthesis, precluding further seedling establishment.

Silvicultural treatment, and its associated disturbance, is likely to influence not only light intensity but also soil fertility. In the Norway maple plantation of Experiment 1 thinning appeared to lead to higher levels of soil mineralisable nitrogen (Section 6.3). In Experiment 2 the thinning and fertilisation treatments appeared to interact to influence dark phase PAR, arguably the most important environmental variable measured in the experimental programme. Thinning still had a positive influence on the establishment of introduced species, even when the influence of the light climate appeared secondary to that of the soil environment, as was the case in the Italian alder plantation of Experiment 1. Thinning operations will also influence environmental variables not representative of the light climate or soil environment, which will influence ground flora response. The current experimental programme has demonstrated that ground flora introductions are possible over a wide range of light and soil conditions, but response may be influenced by competition and other site variables, such as litter cover (Section 6.5).

6.5 The influence of vegetation environmental variables on field layer development

Measured environmental variables, which do not represent the light climate or soil fertility, are only of consequence in field Experiments 1 and 2. These variables have previously been described as 'vegetation environmental variables', as they represent the physical environment for establishment and consist of percentage cover of litter, bare ground and bryophytes. The estimated optimal ranges for these vegetation environmental variables are given in Table 6.3. The establishment environment in Experiment 3 was uniform with 100% bare ground and no litter or bryophyte cover. Litter and bryophyte cover development during the experiment was negligible. The removal of vegetation environmental variables from the establishment environment, including spontaneous vegetation, and the standardisation of other environmental variables in the controlled climate of the polytunnel, allowed the effects of light intensity and soil fertility on the ground flora communities to be the main focus of the experiment. However, the spontaneous vegetation was only harvested above-ground and re-growth coupled with probable recruitment from the weed seedbank, in the soil component of the compost in Experiment 3, rapidly replenished the spontaneous vegetation after its removal. This removal of the initial weed flora not only allowed the establishment of target communities and species, but also the investigation of competition with non-target ruderal species, as is often the case in urban secondary woodlands.

Table 6.3 Between-experiment comparison of estimated optimal ranges for vegetation environmental variables (measured in 1999). Variables considered major determinants of ground flora development are highlighted in bold.

Environmental variable	Experiment 1 Norway maple	Experiment 1 Italian alder	Experiment 2
Bryophyte cover (%)	**11-41**	1-11	**10-40**
Litter cover (%)	25-45	2-5	**15-40**
Bare ground (%)	2-5	2-5	**10-40**

The deep litter layer in the Italian alder stand of Experiment 1 was raked off (Table 6.3), eliminating the heterogeneous niche space, which was created by the litter cover in Experiment 2. The relative density response of the introduced species across the field experiments shows that the Italian alder plantation supported approximately twice the density of introduced species supported at Nedge Hill and that the Norway maple plantation supported approximately twice that of the Italian alder plantation. The smaller response of the introduced species at Nedge Hill can be explained by the litter layer limiting available niche space, and by the lower summer light levels, afforded by the lack of edge effects. Although the influence of the litter layer was much reduced by raking in the Italian alder plantation, the response of the introduced species was tempered by competition from the vigorous background vegetation. However, in the Norway maple plantation, competition from background vegetation was severely limited by the dense shade cast by the pre-establishment canopy. Therefore, once the canopy was thinned, introduced species had no obstacles to community domination.

The canopy of Experiment 2 was more established and complex (with a shrub layer) than the unstructured, monospecific canopies of Experiment 1. As tree species composition affects the amount and type of litter produced (e.g. Bockheim *et al.*, 1991), a more complex canopy will give rise to more complex surface conditions, as was the case in Experiment 2. Experiment 2 had a heterogeneous litter cover and a mosaic of spontaneous tall and short herb forms, whereas Experiment 1 had a sparse spontaneous field layer in the Norway maple stand and a sparse, homogenised (raked) litter layer in the Italian alder stand. Field layer vegetation also produces its own litter effects (e.g. Jandl *et al.*, 1997). As with canopy composition, a complex spontaneous field layer will create a heterogeneous litter layer.

Litter alters the physical and chemical environment; it intercepts light, reduces the soil thermal amplitude and soil evaporation, yet it also intercepts rainfall causing drought stress (Facelli and Pickett, 1991). Petersen and Philipp (2001) concluded that soil droughting in the absence of a litter layer caused localised extinctions in an introduced woodland ground flora. Litter causes organic matter accumulation, enhances decomposition processes, including augmenting soil micro-biota diversity. It also affects pH and nutrient mineralisation (e.g. Gower and Son, 1992; Raulund-Rasmussen and Vejre, 1995). The accumulation of soil organic matter increases cation-exchange capacity, lowers pH and increases water and nutrient holding capacity, especially for nitrogen. Thus, a heterogeneous litter layer provides heterogeneous physical and chemical niche space. The physical niche microclimate amelioration and enhanced soil fertility afforded by moderate litter cover (Table 6.3) appears to favour ground flora introductions. However, under dense litter cover, both light and water stress are likely to limit the establishment of introduced species (Facelli and Pickett, 1991).

The effects of plot position in Experiment 2 were identified as being associated with two slopes acting in two directions: a main north-westerly slope and an apparently secondary south-westerly slope. Slope influenced spatial distributions of litter and bare ground and possibly bryophytes. More bryophytes were found at the top of the main slope, where perhaps litter accumulation was not significant enough to inhibit their growth. Litter and therefore organic matter and nutrients build up down-slope. The main slope was correlated with a background pH gradient, which was probably linked to litter and soil organic matter distributions. However, litter cover was more strongly associated with the secondary slope, where it was inversely related to mineralisable nitrogen, the most importance aspect of soil fertility in Experiment 2. Litter cover in Experiment 2 was apparently related to pH and nitrogen mineralisation (Section 6.3), which together defined niche space and formed a major determinant of field layer development in Experiment 2.

Each target species varied in its response to variations in litter cover. Litter depth could also be a factor (Facelli and Pickett, 1991), but this variable was not measured in the current study. Litter type would probably be fairly uniform in the mixed plantation of Experiment 2. However, localised microclimates could be influenced by litter type (e.g. Bockheim *et al.*, 1991; Graae and Heskjaer, 1997); again this variable was not considered in the current study. The physical barrier that litter provides means that only adapted

species, such as *Hyacinthoides non-scripta,* are likely to be successful at higher cover. The positive association of this species with litter cover in Experiment 2 illustrates this point. The experimental evidence suggests that some litter cover is desirable for niche microclimate amelioration, enhanced germination and establishment of target species. The wide optimal ranges estimated in Table 6.3 suggest that moderate litter cover is ideal, and should be aimed for across much of a site.

Bryophyte cover apparently played an important role in niche microclimate amelioration, and therefore in the success of introduced species in the Norway maple plantation in Experiment 1. Bryophyte mats may trap water and nutrients and organic matter, as well as providing shelter with reduced wind speeds and raised surface temperatures. The spatial heterogeneity of soil nutrients often reflects the spatial heterogeneity of organic matter deposition (Vaz, 2001). The physical effect that bryophyte cover may have on concentrating organic matter is likely to lead to localised enhanced nutrient status. It seems likely that in established woodlands the litter layer would represent the major source of organic matter deposition, but in certain cases, bryophyte cover can influence this. Bryophyte cover may become an important factor in the spatial heterogeneity of establishment niches, when the litter layer is homogeneous or when physical niche amelioration is needed to facilitate species introductions, e.g. on compacted soil. However, the former was not supported by results from the Italian alder plantation in Experiment 1 where bryophyte cover was not correlated with plant distribution. This may indicate that introduced species were simply occupying niche space not already occupied by bryophytes. The 'optimal range' of bryophyte cover suggested by the results of the whole experimental programme was 10-40% (Table 6.3). Higher bryophyte cover was associated with the unfavourable summer light climate of control plots in the Norway maple plantation (Experiment 1). However, in Experiment 2, higher bryophyte cover was associated with fertilised plots.

Thinning operations affected the spatial distributions of litter, bare ground and bryophytes, generally causing a reduction in cover. Reader and Bricker (1994) reported increased exposure of bare mineral soil following canopy thinning, but in the present experimental programme thinning resulted in less bare ground, perhaps due to the homogenisation of the litter layer. Selective canopy thinning adds to the niche heterogeneity of a site, which is likely to be a positive attribute for the establishment of introduced species. However, given the apparently important role that these variables

play in providing suitable establishment environments for ground flora introductions, these variables need to be surveyed before management is undertaken. Silvicultural operations can be carefully planned to maximise areas with 'optimal ranges' of these variables (Table 6.3), within a mosaic comprising the full range of these variables occurring on the site (Section 6.6).

Canopy species composition may be a major determinant of field layer development in secondary woodlands, as it will influence the nature and extent of the litter layer, partly dictating available niche space (physical and chemical). Canopy species will also determine the influence of canopy architecture on the light climate experienced by the ground flora. The extent to which canopy species determine environmental conditions in the field layer is likely to be exaggerated in small monospecific plantations, such as those at the Wolverhampton Environment Centre and diluted in larger, more developed, mixed plantations with more complex soil conditions, hydrology and topography, such as at Nedge Hill. The experimental programme found that canopy species explained major variation in the distribution of field layer plants in Experiment 1 at the Wolverhampton Environment Centre and that background soil and topographic variables were most correlated with ground flora vegetation in Experiment 2 at Nedge Hill.

The evidence suggests that while thinning may influence the light climate and therefore ground flora response, the associated disturbance of the litter layer may play a greater role in influencing the establishment of subsequent ground flora introductions in an established secondary woodland, such as at Nedge Hill. This conclusion contrasts with the results from Experiment 1 at the Wolverhampton Environment Centre, where simple stand structure and more uniform background environmental variation allowed the full effects of thinning to be realised. The increased age and complexity of the canopy (in terms of composition and structure), plus the background slope effects on litter cover, pH and mineralisable nitrogen and the fact that the ground was not raked prior to sowing, may partly explain the reduced thinning effect at Nedge Hill. However, despite the complex background environmental influences on ground flora development at Nedge Hill, thinning still enhanced ground flora response.

6.6 Management implications

The present study has implications for the creation of new woodlands with field layers which better resemble ancient semi-natural target communities (Section 1.4.1). It also has implications for the management of existing secondary woodlands. Management of existing secondary woodlands can be by canopy thinning to manipulate light climate, either to favour existing desirable ground flora communities, or to promote the establishment of introduced species in ground flora enhancement schemes.

6.6.1 Litter and other vegetation environmental variables

The results of field Experiments 1 and 2 suggest that the percentage cover of litter, bare ground and bryophytes, plus the effect that any silvicultural treatment could have on these 'vegetation environmental variables', will influence available germination niches for ground flora introductions. Therefore, these vegetation environmental variables need to be considered when surveying a site for potential ground flora enhancement. Optimal ranges of the vegetation environmental variables have been estimated in the experimental programme (Table 6.3) and extremes were regarded as values falling outside of these ranges. Management guidance could be that extremes, i.e. < 10% litter cover and > 50%, are best avoided across large areas of the site (i.e. they should not occupy > 25% of the site), but that it is desirable that they should exist at low levels in the mosaic of cover, enhancing niche heterogeneity. This will ultimately maximise vegetation heterogeneity, creating more naturalistic and representative target communities (Section 1.4.1). Raking of litter, as was undertaken in the Italian alder plantation of Experiment 1, is not practical on large scales and is unlikely to be necessary in all but the most extreme situations. Evidence from field Experiments 1 and 2 suggests that the disturbance due to thinning operations will considerably reduce litter cover. Site managers could plan thinning operations in such a way that litter cover is also affected in unthinned plots to increase the mosaic effect and maximise niche heterogeneity, e.g. by careful siting of extraction routes.

Evidence from the current experimental programme suggests that the potential competition from spontaneous vegetation needs to be carefully considered when undertaking a site survey. The species composition of the spontaneous vegetation should be surveyed. The functional (Grime *et al.*, 1988) and taxonomic groupings (Stace, 1997) of the species present should indicate whether it is advisable to retain them or to suppress them with a herbicide pre-treatment (Cohn 1994). Wherever possible, woodland species,

even vigorous ones such as *Geum urbanum* and *Rubus fruticosus* agg., should be retained as they form an integral part of target communities (Section 1.4.1), provide a heterogeneous establishment environment and may afford some niche microclimate amelioration. Results from Experiment 2 suggest that certain spontaneous species may be useful in providing a surrogate canopy in high light environments that can temporarily arise from thinning operations (Section 6.2). In general terms, most non-woodland species will not thrive in the longer-term in woodlands, due to light stress. Cohn (1994) found, of the existing pre-establishment vegetation, that the non-woodland grasses were the biggest competitive threat to ground flora introductions, and would necessitate herbicide pre-treatment when present at high covers. Experimental evidence, e.g. from the Italian alder plantation of Experiment 1 and Experiment 2, suggest that ground flora introductions can be successful even in competition with vigorous spontaneous vegetation.

The existing tree canopy will affect the amount and type of litter produced (Bockheim *et al.*, 1991), the amount and type of light reaching the field layer (Mitchell, 1992), water budgets (Price and Watters, 1989) plus nutrient cycling and soil fertility (Gower and Son, 1992; Raulund-Rasmussen and Vejre, 1995). In Experiment 1 the effects of the tree canopy species were interpreted in both plantations as explaining the major variation in field layer species composition. Therefore, a survey of the existing tree canopy by species and percentage cover in the tree, shrub and field layers is essential when contemplating ground flora enhancement. Many urban secondary woodlands include non-native species or exotic varieties, or species outside of their natural range. If possible thinning operations should be planned to achieve a more naturalistic canopy, i.e. one which is more representative of the target community (Section 1.4.1). Results from the Italian alder plantation of Experiment 1 perhaps suggest that sites with a high percentage of alder species should be avoided on fertile soils, as their nitrogen fixing capabilities are likely to increase soil fertility.

6.6.2 Light climate

Evidence from the current experimental programme suggests that light climate will be an important factor in field layer development. Light climate could, in terms of establishment environment, be the most important factor in a ground flora enhancement scheme. The prevailing spatial light climate which will be experienced by the field layer plants therefore needs to be measured. In field Experiments 1 and 2 percentage canopy

cover provided a reasonable inverse analogue for light intensity, however, dark phase PAR was generally the most important aspect of the measured light climate. It has been concluded, from the results of the experimental programme, that dark phase PAR (expressed as a percentage of ambient PAR) is a useful indicator of the complex woodland light climate, which will affect the establishment of ground flora introductions.

Selective canopy thinning may be considered as a method for altering the spatial light climate. Results from Experiment 1 illustrate the importance of accounting for the likely edge effects and the limited treatment window, afforded by small treatment plots, when planning thinning operations. Follow-up management needs to be planned and the likely consequences estimated. The effects of disturbance from thinning operations, e.g. on the distribution of litter and bare ground should be considered. Careful planning of silvicultural operations can make use of these effects and maximise habitat and niche heterogeneity. For example, this can be done by targeted siting of extraction routes. An average range of between 5-20% summer infiltration of PAR would be desirable in thinned areas (Section 6.2).

6.6.3 Soil fertility

Optimum soil fertility levels for ground flora introductions were difficult to recommend from the present study (Table 6.2), as most species grew well throughout the full range of fertility conditions found in the experimental programme. Soil conditions across much of the experimental programme were believed to be close to optimum for ground flora introductions, and generally did not reflect extreme conditions, which would have been unfavourable to species introductions (Quist, 1995). The macronutrient limits and ranges recommended for species-rich grassland restoration (< 70 mg kg^{-1} extractable phosphorus, < 300 mg kg^{-1} extractable potassium and 10-100 mg kg^{-1} mineralisable nitrogen (McCrea *et al.*, 2001b; Vaz, 2001) may provide useful guidelines for ground flora enhancement schemes. However, it seems likely that in practice woodland field layers are far more resilient to high levels of soil fertility than grassland systems (Kirby, 1997). This is at least partly due to the overriding light stress in woodlands (Packham *et al.*, 1992), which can negate the effects of excessive soil fertility. Nevertheless, intra-site variation in aspects of soil fertility within optimum ranges can influence field layer development. Evidence from Experiment 2 showed that background variations in mineralisable nitrogen and pH, associated with site topography, were strongly correlated with plant distribution in the field layer. In the Italian alder plantation of Experiment 1

soil nitrogen, phosphorus and potassium, probably related to the nitrogen fixing capabilities of the alder trees, were associated with ground flora species composition. This evidence supports the findings of Fitter and Setters (1988), who found that localised spatial variation in aspects of soil fertility influenced the intra-site heterogeneity of the field layer response.

The above discussion suggests that it would be sensible to measure baseline soil fertility when planning ground flora enhancement schemes. This need not be a large-scale expensive survey. Initially the soil series on a site should be identified and soil distribution maps and series descriptions should be referred to (e.g. Ragg *et al.*, 1984, for the West Midlands region). At least one bulked sample (consisting of at least 5 sub-samples and preferably 25) should be taken from a 'W-shaped walk' across the area occupied by each soil series. Also separate samples should be taken from areas which have a marked change in vegetation and / or drainage and topography. The spatial mapping of soil parameters in the field experiments provided a valuable tool for visualising the intra-site heterogeneity of the soil environment. More practical advice on site selection, in terms of soil fertility, would be to spatially map soil types and fertility levels, and to favour sites with more uniform nutrient distributions, or at least avoid those that have considerable areas of extreme soil chemical conditions. Such sites may require levels of pre-treatment and amelioration not considered in this study (e.g. Fee *et al.*, 1996; Gilbert and Anderson, 1998).

Ground flora enhancement in secondary woodlands may be considered if all of the significant environmental variables (i.e. extractable phosphorus, extractable potassium, mineralisable nitrogen, pH, percentage cover of litter, bare ground and bryophytes) fall within the optimum ranges suggested (Tables 6.1-6.3), or if no more than 25% of the site is sub-optimal for any of these variables. The light climate can of course be manipulated by thinning. Manipulation of soil fertility is likely to be far more difficult and perhaps unethical.

The manipulation of woodland soil fertility to reduce fertility is unlikely to be practical in secondary woodlands, unless coppicing is part of the management plan. Arable cropping will only be possible prior to tree planting in new woodlands and results in grassland creation schemes are inconsistent, especially in terms of reducing residual phosphates (e.g. Marrs, 1993; McCrea *et al.*, 2001a). It would seem that reduction to desirable

phosphorus levels is only possible if initial levels are not well in excess of optimal. Conversely, fertilisation to ameliorate impoverished establishment conditions, e.g. Fee *et al.* (1996) on infertile colliery spoil, may be essential for the successful establishment of ground flora introductions. Results from the current experimental programme suggest that fertilisation of timber crops in forestry operations may not seriously impede the establishment of introduced field layer species, and may in fact be beneficial in the absence of competition from non-woodland ruderals. However, fertilisation in many enriched urban situations, is likely to be detrimental to the persistence of ground flora introductions as competition from non-woodland ruderals will be enhanced.

6.6.4 Environmental heterogeneity

A mosaic of environmental conditions will provide the heterogeneity representative of target communities (Section 1.4.1). In secondary woodland sites this situation is already likely to exist and can be enhanced by carefully planned silvicultural operations. Selective thinning can be used to bring average dark phase PAR (and hence average light phase PAR) within optimal ranges. If resources are limited, only thinned areas could be sown while giving due consideration to the minimal colonisation capabilities of woodland plants (e.g. Dzwonko, 2001; Verheyen and Hermy, 2001). Particular care is needed on sites that are contiguous with or adjacent to ancient semi-natural woodland, which are likely to be designated sites (statutory and non-statutory), so as not to cause genetic contamination of these sites. This scenario requires native seed of local provenance, which in this case should probably be gathered from the adjacent ancient woodland site (Section 6.7).

Suitable species for ground flora enhancement and optimal introduction methods recommended by Cohn (1994) were used in the current study. Only species which Cohn (1994) found could be successfully introduced into secondary woodlands by seed were used. Results from the field experiments support the findings of Cohn (1994) in demonstrating that woodland ground flora can be successfully introduced into existing secondary woodland communities, without use of a herbicide pretreatment and into relatively vigorous established vegetation. Results from the current experimental programme showed that ground flora introductions were possible over a wide range of light and soil conditions, but that response may be influenced by competition and other site variables, such as litter cover (Section 6.5).

6.7 Limitations and further work

The main limitation of the present study was the short time-span necessitated by the funding. The established experiments will, however continue to generate results, which will contribute to longer-term studies of woodland ecology. The edge effects and minimal treatment window (where the effect of thinning on light climate was short-lived due to canopy expansion from adjacent plot edges) in Experiment 1, were partially negated in Experiment 2 by the larger plot size and 'whole wood' buffer zone. The slope effects in Experiment 2 were only eliminated in one direction by the randomised block design. Blocks were established along the main north-westerly slope, which turned out to be secondary to the south-westerly slope in terms of the effects on associated environmental variables and the predicted influence on the field layer vegetation. This illustrates the importance of predicting and minimising background environmental effects when designing field experiments. Experimental treatment effects must have been masked to some extent in Experiment 2 by these background environmental gradients. This experiment does however still provide valuable insight into woodland processes. The unavoidable difference in survey dates between the two seasons in the field experiments may not have had a major impact on plant community composition. Kirby *et al.* (1986) showed that differences between survey data collected in April-May and August-September in three British woodlands were not in the species found, but in the frequency with which they were recorded.

Measurement of the complex woodland light climate and quantification of the ground flora response was achieved by measuring light intensity in the form of average PAR (expressed as a percentage of ambient levels) during the woodland light and dark phases. The use of this measure of the woodland light climate was simple, robust and allowed meaningful comparisons to be made between sites and with other environmental variables, such as those representing soil fertility. The current research also showed that percentage canopy cover was negatively correlated with PAR providing an inverse analogue for light intensity, although this was only demonstrated on an intra-site basis and inter-site use would probably require some form of species calibration.

Although the results from the current study are extremely persuasive, the possibility that there is an unmeasured and influential component of the complex woodland light climate which is not directly correlated with irradiance must not be overlooked. Therefore, further work is needed on measurement of the complex woodland light climate and

quantification of the ground flora response. Further work has already been initiated, using HemiView software (Delta-T Devices Ltd., 1998, 1999) to allow rapid computerised analyses of hemispherical photographs taken during both the woodland light and dark phases. HemiView enables prediction of many aspects of the woodland light climate, which to some extent are dependent on canopy architecture, e.g. sunfleck duration, the measurement of which was not possible during the current research. These aspects of the woodland light climate will be used as explanatory variables in CANOCO vegetation analyses, as undertaken in this research. Further investigation of light as an ecological factor will enable identification of those aspects of the light climate which have most influence on ground flora development. Ground truthing of significant variables predicted by HemiView by calibration with PAR measurements from the current study will allow robust inter-site comparisons of woodland light climates.

Although conclusions from the soil data were limited by the single 'snap-shot' survey carried out in the experimental programme, more frequent sampling was beyond the scope of this research. The soil sampling and chemical analyses carried out in the experimental programme gave a useful indication of baseline soil conditions, plus treatment effects, and provided an estimate of soil fertility, all of which could be correlated with ground flora vegetation. The soil variables recorded were comparable within and between-sites and were measured on scales that allowed direct comparison of vegetation effects between variables.

Vaz (2001) suggested that total nitrogen may be a more useful indicator of site soil conditions, with respect to grassland creation, than mineralisable nitrogen. However, mineralisable nitrogen may provide a proxy measure for the development and activity of the soil micro-biota, the quantification of which was beyond the scope of the current research. The measurement of soil moisture could be a useful addition to future surveys. DeMars and Runckle (1992) found soil moisture to be a major determinant of field layer development during secondary succession and Vaz (2001) cited the importance of this variable in mitigating the effects of excessive fertility, particularly available potassium in grasslands. The use of Ellenberg's indicator values as a proxy measure for ground flora response to soil fertility requires further investigation. Results for woodland forbs gained by Meerts (1997) were encouraging; the species N index allowing the prediction of nitrogen and phosphorus foliar concentrations with the R index correlating with foliar potassium concentrations.

The problem of obtaining inexpensive and viable seed of local provenance is perhaps the biggest obstacle to the widespread and large-scale application of ground flora enhancement. There is considerable demand, for example from agri-environment schemes, for such seed for grassland restoration, although many issues remain, including variety, ecotype and provenance. However, at present the scale of demand for woodland species from seed merchants is insufficient to increase supply and improve provenance. Hand-collection of seed, as employed in the current experimental programme, is clearly not applicable to large-scale restoration schemes. Although not directly addressed by the current research, the problems surrounding seed acquisition, for woodland ground flora enhancement schemes, warrant further investigation.

The method of strewing green hay (Trueman *et al.*, 1994) can be used to overcome the problems of provenance, ecotype and variety in grassland creation and enhancement schemes, and has allowed the introduction of a range of species much wider than that readily available from seed merchants. Full mechanisation of the hay strewing method is currently being perfected. Harvesting seed from ancient woodland plants on a large scale raises a number of issues. Perhaps hedge-bank vegetation could be used to provide a local source of woodland herb seed, if conditions in the receiver woodland (light and fertility) are conducive to the woodland herbs over and above the non-woodland grasses. The vegetation could be harvested at the time of maximum seed ripening and strewn the same day in the receiver woodland, as with the hay strewing technique. However, there are potential problems with this technique mainly relating to the differing phenologies of woodland and woodland edge species. For example, the optimum seed collection point is likely to be different in different species; unlike in a traditional hay meadow where plant ecotypes are all adapted to the same cutting date. This may mean using several cuts and inoculations. This 'hedge strewing' technique has been little researched to date, although there are plans to investigate the methodology within the University of Wolverhampton Habitat Creation and Vegetation Ecology Research Group (Cohn pers comm., 2000).

Ground flora enhancement by hand-application of seed is not practical on a large scale. The mechanisation of the process, and implicit cost reduction, require investigation to enable this technique to be economically and practically viable in large woodland restoration schemes. The use of 'inocula', employed in grassland enhancement (e.g. Gilbert and Anderson, 1998), might allow targeting of scarce resources to areas of optimal environmental conditions, but the extremely poor colonising and spreading

abilities of some woodland herbs (Section 1.3) will preclude spread from these areas in all but the very long-term.

In attempting to make woodland ground flora enhancement economically and practically viable, the establishment of ground flora via seeding could be carried out at the same time as tree planting. In terms of introducing ground flora species into new woodland plantings, a single operation will reduce costs and management problems and accord with the funding and monitoring mechanisms that often make such schemes possible. However, conventional wisdom on ground flora enhancement (e.g. Boorman, 1990; Fu and Buckley, 1991; Francis *et al.*, 1992; Street and Mond, 1992) suggests that species introductions should be made after canopy closure. This usually occurs when the plantation is *c.* 10 years old, depending on species, planting regime and site conditions. A closed tree canopy provides a light climate that is likely to competitively favour the shade-tolerant woodland herbs over the more light-demanding species, such as the non-woodland grasses. The shade stress afforded by a closed canopy is likely to be even more important when introducing ground flora species into fertile urban sites. The establishment of introduced species in the high-light environment of ride-side thinned plots in Experiment 1, in competition with vigorous ruderals, illustrates the possibility of making ground flora introductions without a closed canopy.

The feasibility of introducing ground flora species into new woodlands where there is strong competition from nitrophilous species and no initial canopy is already being investigated. The greatest competitive threat to ground flora introductions, and indeed to young trees, is likely to come from the non-woodland grasses (Cohn and Packham, 1993), which, unless soil fertility is limiting, are likely to thrive in the high light environment of a new woodland planting. Early results from an experiment established at the University of Wolverhampton Plant and Environment Research Unit are promising and will be published as part of a wider study.

The use of nurse crops in grassland restoration is well documented (e.g. Gilbert and Anderson, 1998), but remains little researched in woodland ground flora enhancement. Nurse species in grassland restoration are usually relatively short-lived or non-persistent species sown with or prior to the target species. They usually serve the role of ameliorating harsh niche microclimates to aid germination and establishment of target species. In a woodland environment, the additional role of providing a surrogate canopy

can be performed by a nurse species. The potential of using either a target species, such as *Silene dioica,* or a spontaneous species, like *Urtica dioica,* as a nurse species in woodland ground flora enhancement schemes warrants further investigation.

Tall herb species, such as *Silene dioica,* may provide a surrogate canopy to the smaller and perhaps slower-establishing woodland herbs. *Silene dioica* could be a candidate for such as role, as it rapidly establishes itself across a very wide range of ecological conditions (Slade and Causton, 1979; Matlack, 1987). The *Silene* die back (apparently caused by fungal attack due to lack of airflow) which occurred in the lowest light treatment in Experiment 3, constrains the full range of environments in which this species can thrive. *Silene dioica* can effectively respond to increases in light climate or mineral nutrient supply when the other is limiting (Cohn, 1994), and should establish in any English site suitable for ground flora enhancement. *Silene dioica* may dominate communities after establishment, preventing other target species from occupying germination niches. However, long-term studies (Cohn *et al.*, 2000) have indicated that *Silene dioica* is likely to lose its vigour after several years. This tendency also makes for a suitable nurse species. A nurse species acting as a surrogate canopy will ameliorate niche microclimates, enhancing success of other target species, including provision of shade stress to the non-woodland competitors. Shade provision may be particularly useful when establishing ground floras in high light environments, such as when tree planting and ground flora introduction are carried out in the same operation, or season.

Spontaneous tall-herb species, such as *Urtica dioica*, which are likely to be prevalent in the high fertility soils typical of many urban and former-arable substrates, could provide an ideal surrogate canopy for ground flora introductions. *Urtica* is only moderately shade-tolerant (Pigott, 1971), and although it may be able to persist in dense shade if soil fertility is sufficiently high, its differing phenology means that it is not usually in direct competition with the introduced woodland species. Unlike *Silene dioica*, the phenology of *Urtica dioica* allows vernal species to flower before canopy closure and then provides shade to put non-woodland light-demanding species at a competitive disadvantage. *Urtica* itself is not necessarily a competitive threat to target species where stands are not so dense as to minimise niche availability to other species. However, Verheyen and Hermy (2001) found that the presence of *Urtica dioica* restricted colonisation by ancient woodland herbs in a secondary deciduous forest in Belgium. The balance between nurse species density and available germination niches warrants further investigation in

woodlands. The long-term fate of the nurse crop and its impact on target species also requires investigation. The extent to which a surrogate canopy alters the light climate, both spatially and temporally, needs investigating with respect to ground flora development.

The importance of mycorrhizal associations to the success of species introductions in secondary woodland warrants further investigation. Most woodland herbs are known to form, and benefit nutritionally from, mycorrhizal associations in the field (e.g. Merryweather and Fitter, 1995a,b; Hodge *et al.*, 1998, 2000). *Silene dioica* is an exception, being the only species introduced in the experimental programme which is not known to usually form such associations (Merryweather, pers. comm., 2001). However, the obligate mycorrhizal symbiont *Hyacinthoides non-scripta* (Merryweather and Fitter, 1995b, 1996), has been successfully introduced by seed in this and other studies (e.g. Francis *et al.*, 1992; Cohn, 1994). New woodland soils are known to have poorly developed structure (Packham *et al.*, 1992) and decomposition subsystems and are presumed to have equally poorly developed mycorrhizal soil communities. This is certainly the case in grassland ecosystems, where ancient semi-natural habitats usually have a well-developed and diverse soil fauna with the fungal component being most important in decomposition pathways. In contrast, frequently disturbed arable (and improved grassland) soils tend to have an under-developed fungal flora with bacterial pathways dominating the decomposition subsystem (Bardgett *et al.*, 1996 and Bardgett and McAlister, 1999).

It might follow from this that new woodlands planted on former-arable soils are likely to have an impoverished soil fungal component, which could adversely affect ground flora species introductions. It seems unlikely that cleaned dried seed from a merchant could convey mycorrhizal inocula. However, the situation in woodlands is complicated by the presence of trees, many of which form mycorrhizal associations. It seems more probable that mycorrhiza could be introduced with trees rather than seed. However, these species are more likely to be associated with tree species than the introduced ground flora plants. Soil development in new woodlands, particularly the mycorrhizal component and its implications for ground flora enhancement needs further research. Soil spreading, from ancient semi-natural woodland, or 'hedge strewing' could accelerate the process of inoculum introduction (as hay strewing is believed to do in grassland restoration schemes). However, evidence of species success from ground flora enhancement studies

to date suggests that inoculation in the field is unnecessary, even for the establishment of obligate species like *Hyacinthoides non-scripta*.

6.8 Conclusions

- Woodland ground flora can be successfully introduced into existing secondary woodland communities, without use of a herbicide pretreatment and into relatively vigorous established vegetation, supporting the findings of Cohn (1994).

- Light intensity, measured in a form available to field layer plants, i.e. PAR, is always a major determinant of ground flora development. Once site baseline light climate has been ascertained, light intensity can be manipulated by selective thinning. In the present study the highest ground flora establishment rates were achieved with an average summer light climate of between 5-20% of ambient PAR after thinning. This was achieved in the experimental programme by thinning to 50% cover from varied canopy starting points.

- Any annual non-woodland species which may rapidly colonise thinned plots are unlikely to persist, and therefore do not pose a management problem. The combination of increased irradiance and disturbance created by thinning also encourages colonisation by cosmopolitan non-woodland and woodland edge perennial herbs. These species should not be allowed to colonise in large numbers during the establishment phase, as they may out-compete the introduced species. This situation is best avoided by provision of e.g. a large buffer zone, ensuring adequate distance from non-target seed sources.

- The potential for colonisation by non-woodland species from the soil seedbank should not be underestimated. Clues to this potential may lie in the woodland's age, size, management history, surrounding land-use, and in the spontaneous field layer vegetation. If the potential for colonisation from the soil seedbank is high then it may be prudent to undertake seedbank trials before embarking on a programme of ground flora enhancement. If perennial non-woodland herbs do become established then chemical control (spot treatment) will have to be considered. However, careful site selection and management should ideally prevent this situation from occurring.

- Background soil fertility, and its spatial variation, needs to be taken into account when planning ground flora enhancement schemes. Background soil fertility depends largely on soil type and history, tree canopy and litter distribution.

- Fertility alone may not be an obstacle to ground flora enhancement if plantations are buffered and large enough to minimise invasion by aggressive non-woodland and woodland edge species. For example, where high soil fertility combines with light edge effects, perennial grasses may dominate the field layer. Small plots on fertile substrates in urban situations, where vandalism may keep a plantation open (e.g. by tree burning or felling), may be particularly at risk from invasion by non-woodland grasses. These may need a herbicide pre-treatment to provide establishment niches for introduced species.

- Thinning and fertilisation appear to encourage the establishment of introduced species within available niches. Thinning influences light intensity, soil fertility (e.g. it increases mineralisable nitrogen) and other environmental variables which combine to determine niche space. Light regime is easier and more practical to influence than soil fertility. In practice, fertiliser additions in urban secondary woodlands are likely to prove 'unethical' for a variety of reasons, including cost and eutrophication.

- Disturbance associated with thinning coupled with open spontaneous vegetation, positively influenced ground flora species introductions in the experimental programme. Disturbance of thick litter layers, associated with thinning operations, may be insufficient to significantly alter establishment patterns. In such cases, the influence of the increased irradiance, following thinning, is likely to be secondary to that of niche availability created by the spatial variation in the litter layer. In extreme cases selective removal of the litter layer, e.g. by raking, may be required to create germination niches. Optimal litter cover is 5-40%; however, a mosaic effect should be sought. The presence of deep litter or established vegetation will compromise the positive effects of thinning on enhanced ground floras. Thinning should be used to augment the existing niche heterogeneity provided by the litter layer and spontaneous vegetation.

- The heterogeneous niche space provided by the background vegetation, including the surrogate canopy effect afforded by tall herbs, should be maximised. Any use of herbicide pre-treatment will deny this opportunity. Retention of existing background

vegetation will provide elements of a semi-natural community, such as *Rubus fruticosus* agg., which would not be introduced in an enhancement scheme.

- Niche heterogeneity increases with woodland succession. Management should be used to enhance this heterogeneity, while providing optimal environmental conditions within available niche space to maximise establishment success of ground flora introductions.

- In the experimental programme light intensity and soil fertility were manipulated and measured on scales which enabled detection of common ground flora responses at species and community levels (including effects in combination and interaction) from the controlled environment of the polytunnel to the heterogeneous environment of a mixed canopy secondary woodland at Nedge Hill. This has enabled estimation of optimal ranges for light intensity and soil fertility plus significant vegetation environmental variables (Tables 6.1-6.3), as well as prediction of the relative significance of these environmental variables.

- Cohn (1994) identified suitable species and introduction methods for woodland ground flora enhancement schemes and identified situations where ground pre-treatment would be advisable. The scope of the present research did not encompass the above variables, but concentrated on the hypothesis that the influence of soil fertility and light intensity at establishment would be crucial for the success of ground flora enhancement schemes Cohn (1994). The current research has shown that light climate at establishment is always a major determinant of field layer development. Dark phase PAR seems to be the most important aspect of the measured light climate. Soil fertility does influence ground flora development, but its effects are usually secondary to light intensity. The relative importance of different aspects of soil fertility varies between sites and is less predictable than those of the light climate. The woodland species introduced in this study can thrive over a wide range of soil fertility conditions (Table 6.2). If management of the light climate and other site conditions are suitable for ground flora introductions, then soil fertility, unless extreme, should not be an obstacle to successful establishment.

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